Effects of Anthropogenic Noise and Light on the Vocal and Spatial Behaviour of Birds

by

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ABSTRACT

Understanding how anthropogenic disturbance affects animal behaviour is challenging because observational studies often involve co-occurring disturbances (*e.g.*, noise, lighting, and roadways), and laboratory experiments often lack ecological validity. During the 2016 and 2017 avian breeding seasons, I tested the effects of anthropogenic noise and light on the singing and spatial behaviour of birds. I independently manipulated the presence of anthropogenic noise and light at 110 sites in an otherwise undisturbed boreal forest in Labrador, Canada. Each stimulus was surrounded by a microphone array that recorded and localized singing birds throughout the stimulus presentation. Results show that noise attracts birds, but that light and the interaction between noise and light have little or no effect. None of the treatments affected when birds began singing. My study provides some of the first experimental evidence of the independent and combined effects of noise and light on the singing and spatial behaviour of wild birds.

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Last, but certainly not least, is Shiva. Peter Matthiessen wrote; “When you see a tiger, it is always like a dream” and the time I spent with you, tiny tiger, was certainly a dream come true." To quote further, “…here I am, safely returned over those peaks from a journey far more beautiful and strange than anything I had hoped for or imagined - how is it that this safe return brings such regret?”

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

Chapter 1: A General Introduction to the Effects of Noise and Light on Birds

Anthropogenic Disturbance

Anthropogenic disturbance is defined as any event in which human activity alters the behaviour, ecology, or evolution of the individual, population, or wildlife community (Smit and Visser 1993). Disturbances take many forms and can impact wildlife directly. For example, toxins released into the environment can poison animals (Harrison et al. 1997), human-wildlife conflicts can result in the harassment and direct killing of large mammalian predators (Green et al. 2018), and towers and powerlines can result in collisions or electrocution (Bernardino et al. 2018). Disturbances can also affect wildlife indirectly. Chemical contamination (Heinrichs et al. 2016; Wilcox et al. 2016), logging (Smith et al. 2000), resource extraction (Walker et al. 1987), and urban development (Whittington et al. 2005) can all degrade, fragment, or destroy animal habitat, which, in turn, can cause population declines (Vors et al. 2007), habitat avoidance (Moran-Lopez et al. 2005), and reproductive failure (Giese et al. 1989).

Within the last century, there has been a growing recognition that noise and light associated with human activity constitute anthropogenic disturbance (Ortega 2012). Noise is unwanted sound, often described as an increase in volume or amplitude that can cause hearing loss, permanent damage, or behavioural consequences such as annoyance, to a subject (Longcore and Rich 2004). Stress induced by noise can produce

long-lasting effects on the structure and function of vertebrate brains, including impairment of learning and memory (Bremner 1999). In humans, a nation-wide survey in Canada revealed that 8% of citizens aged 15 years or older were annoyed by noise and experienced noise-induced stress (Michaud et al. 2005). Survey participants listed traffic noise as the primary source of annoyance. In comparison to people, animal hearing is often more sensitive, especially with respect to high-frequency sounds (Heffner and Heffner 2007). In one study, mice (*Mus musculus*) exposed to aircraft traffic noise (72 dB(A)-85dB(A) SPL) for four days showed increased blood pressure and cortisol levels, relative to control mice that were exposed to white noise broadcast at the same amplitude (Munzel et al. 2017). Animals in laboratories, such as mice, can also suffer fatal seizures in response to loud noise (Turner et al. 2005). Unfortunately, noise pollution is widespread because it is produced by diverse sources, including airplanes, boats, vehicles, and activities related to seismic blasting and construction (Ortega 2012). In addition, most research on the impacts of noise on animal behaviour have focused on traffic noise, with relatively few studies examining the effects of low-amplitude and non-threatening noise (Iglesias-Marchan et al. 2018).

Light pollution, like noise pollution, is a by-product of human activity that can result in ecological and behavioural consequences for wildlife, including changes in circadian rhythms that disrupt sleep patterns (Shannon et al. 2016). Extreme point sources of light, such as urban centres, large shopping malls, and offshore hydrocarbon

platforms make the surrounding artificially illuminated areas up to 200,000 times brighter than nearby undisturbed areas (Montevecchi 2006; Falchi et al. 2011). Most light pollution, however, is associated with less powerful outdoor lighting fixtures, such as street lights and the lights attached to houses and buildings (Kuechly et al. 2012). Watson et al. (2016) measured light intensities associated with low-level urban illumination (0.15 lux), street lighting (5 lux), and parking lots (10 lux) and found that these more modest sources of light were still 15 times brighter than unlit rural areas. In contrast to extreme point sources of light, these more modest sources of light are extremely widespread (Pun et al. 2014). Falchi et al. (2016) found that night-time light pollution covered approximately 80% of the global human-populated terrestrial landmass and was estimated to increase annually by 6% in North America and Europe.

Birds as Bioindicators of Anthropogenic Disturbance

Birds were used as bioindicators of environmental health as early as the 1960s. Rachel Carson's *Silent Spring* vividly depicted the dangers of chemical contamination, using avian models as indicators of the health of the natural world (Carson 1962). Birds are excellent bioindicators of the health of the overall environment, and of the effects of anthropogenic disturbance on animals (Burger and Gochfeld 2001; Gregory and van Strien 2010; Herrera-Duenas et al. 2014). For example, many aerial insectivorous birds have been declining due to suspected decreases in insect populations (Nebel et al. 2010). Such changes in important food sources for birds and other animals have been

linked to anthropogenic disturbance in the form of climate change and agricultural practices, including pesticide use (Bryant et al. 2002).

Part of the success of using birds as bioindicators is that the field-based methods used to study birds are versatile, readily accessible, and relatively inexpensive (Tarlow and Blumstein 2007). Migratory birds often show nest site fidelity among years (Greenwood and Harvey 1982), which allows researchers to track annual survival and longevity. Biological samples, such as feathers, blood, and plasma, can be collected during nesting to estimate recent diet composition and stress and how these might be linked to anthropogenic disturbance experienced during winter (Fowler 1999).

Effects of Anthropogenic Noise on Birds

Anthropogenic noise can have detrimental effects on avian physiology. For example, Brischoux et al. (2017) found that rural House Sparrow (*Passer domesticus*) nestlings exposed to experimental traffic noise throughout the nestling period had significantly lower metabolism in comparison to nestlings raised without exposure to noise. Noise can also reduce reproductive success (Potvin et al. 2016). A long-term study (1995–2009) on Blue Tits (*Cyanistes caeruleus*) showed that females nesting in close proximity to traffic noise produced fewer eggs and fledglings compared to females nesting farther away (Kempenaers et al. 2010). Similarly, Halfwerk et al. (2011a) found that female Great Tits (*Parus major*) produced smaller clutches the closer they nested to

sources of traffic noise, and that fewer young fledged from noisy nest sites than from nests located farther away from noise sources (Halfwerk et al. 2011a).

Anthropogenic noise can also influence many aspects of an animal's behaviour and ecology. First, noise can impair an animal's ability to capture prey (Mason et al. 2016), and thus cause predatory birds to avoid or disappear from noisy, but otherwise productive, habitats (Francis et al. 2009). In captive northern saw-whet owls (*Aegolius acadius*), prey detection and overall hunting success decreased as the level of anthropogenic noise increased (Mason et al. 2016). Second, anthropogenic noise can mask an individual's ability to hear predators and predator-induced alarm calls. As a result, that individual may need to spend more time engaged in anti-predator behaviour and less time engaged in other critical activities, such as foraging and offspring provisioning (Buxton et al. 2017). Female house sparrows, for example, flee approaching predators more frequently when anthropogenic noise is present (Meillere et al. 2015; Shannon et al. 2016). Third, noise can disrupt parent-offspring communication, causing young birds to be ill-provisioned by their parents during crucial times of development (Schroeder et al. 2012). For example, House Sparrow nestlings reared in the presence of noise were fed less by their parents and fledged with lower body masses than chicks reared in the absence of noise (Schroeder et al. 2012). These developmental handicaps may ultimately impair parental reproductive fitness by reducing fledging success and recruitment (Schroeder et al. 2012).

Anthropogenic noise can also interfere with the production and perception of songs, which are sexually selected acoustic signals involved in mate attraction and contest competition in birds (Andersson 1994; Catchpole and Slater 1995). Many bird species begin singing around sunrise, which results in a multi-species chorus known as the ‘dawn chorus.' Noise can disrupt the timing of dawn song in birds and may force birds to advance or delay the onset of singing (Fuller et al. 2007; Cartwright et al. 2014; Dominoni et al. 2016). Wild songbirds living in urban areas, for example, delay the timing of the dawn song to times of the day when there is less exposure to noise (Fuller et al. 2007; Gil et al. 2015). Similarly, urban European Robins (*Erithacus rubecula*) shift the timing of song production to night, when noise is less prevalent (Fuller et al. 2007). Although these temporal shifts reduce the masking effects of noise, they might also make the songs less effective at attracting mates and repelling rivals (Fuller et al. 2007).

In addition to shifting the timing of song production, birds in the presence of noise can change the fine structure of their songs in ways that are thought to increase signal transmission and detectability (Hanna et al. 2011; Cartwright et al. 2014; Gil and Brumm 2014). First, birds can increase the amplitude of their songs in the presence of noise (Brumm and Zollinger 2011). Known as the Lombard Effect, it has been demonstrated in many species, including Nightingales (*Luscinia megarhynchos*; Brumm 2004) and White-throated Sparrows (*Zonotrichia albicollis*; Derryberry et al. 2017).

Second, birds can increase the minimum frequency of their songs, which can minimize the masking effects of low-frequency noise, such as traffic noise. Slabbekoorn and Peet (2003) found that the minimum frequency of songs was higher in Great Tits (*Parus major*) occupying noisy urban territories than in Great Tits occupying quiet rural territories. Third, birds can increase the duration of songs or song elements, which may increase the likelihood of the song being detected, especially in environments where noise is intermittent (Gough et al. 2004). Pacific Wrens (*Troglodytes pacificus*), for example, sing songs with longer syllables when living near loud ocean surf, and longer songs overall when living near noisy highway traffic (Gough et al. 2004). Fourth, birds can also increase the tonality of their songs, which has been demonstrated in Red-winged Blackbirds (*Agelaius phoeniceus*) exposed to low-frequency traffic noise (Hanna et al. 2011). These mechanisms, together with changes in the timing of song production, are not mutually exclusive, and some birds are known to alter multiple acoustic parameters in response to noise (Wood and Yezerinac 2006).

Noise-induced changes to song can be permanent or transient (Nemeth and Brumm 2010; Slabbekoorn 2013). In some species, noise can affect song learning, which has permanent effects on song structure. Captive male Zebra Finches (*Taeniopygia guttata*) that were exposed to noise were unable to learn the correct order of syllables in their songs (Potvin et al. 2016), presumably because the areas of their brains associated with song learning were significantly smaller than in individuals not exposed

to noise (Potvin et al. 2016). In contrast, male House Finches (*Haemorhous mexicanus*) and male Red-winged Blackbirds showed rapid behavioural flexibility by suddenly altering the structure of their songs in the presence of transient experimentally broadcasted noise (Bermudez-Cuamatzin et al. 2010; Hanna et al. 2011).

Finally, anthropogenic noise can influence song perception. In captive Canaries (*Serinus canaria domestica*), females exposed to noise did not exhibit species-typical preferences for low-frequency songs (Aunay et al. 2014). Similarly, Halfwerk et al. (2011b) found that male Great Tits sing their lowest frequency songs when females reach peak fertility, but that low-frequency noise prevents females from exhibiting their normal preference for these low-frequency songs. In this way, noise can mask preferred songs and alter patterns of mate choice. Noise-induced changes to song, combined with modified preferences for noise-modified songs, have even been suggested as a possible mechanism for reproductive isolation and genetic differentiation in urban populations of Great Tits, Dark-eyed Juncos (*Junco hyemalis*), and European Blackbirds (*Turdus merula*; Slabbekoorn and Ripmeester 2008).

Effects of Anthropogenic Light on Birds

Like anthropogenic noise, anthropogenic night lighting can have detrimental effects on avian communities, populations, and individuals. Unlike the impacts of noise, however, the effects of light on birds have been known and documented for centuries.

Hunters in the 18th century lured light-sensitive seabirds to brightly lit fires (Mailliard 1898; Montevecchi 2006), and natural history groups in the 1800s reported thousands of birds colliding with lighthouses (Allen 1880). In the 1960s, Cummings and Hewitt (1964) used intense lighting and a high-powered motorboat to “stun” and capture 1146 waterfowl and waterbirds for research-related purposes.

Collision with artificially lit structures is now recognized as a serious concern for the conservation of many avian species. Seabirds in the Petrel family (*Procellariidae*), for example, are drawn to artificial lights, such as those found on ships and off-shore oil drilling platforms (Montevecchi 2006; Burke et al. 2012). Twenty-six of the 56 petrel species are now listed as 'threatened' on the International Union for Conservation of Nature's Red List (Rodriguez et al. 2017). Juvenile Atlantic Puffins (*Fratercula arctica*) dispersing from their breeding colonies are also attracted to artificially lit buildings, which leads them towards land instead of out to sea (Wilhelm et al. 2013). Dispersing to sea during the cover of darkness provides protection from predators, so disorientation and stranding by artificial light may cause birds to delay dispersal until the following day when there is a greater risk of predation (Wilhelm et al. 2013).

Like seabirds, migratory birds are attracted to and collide with brightly lit structures. Canada's Fatal Light Attraction Program (FLAP) estimates that between 100 million and 1 billion birds die every year from fatal collisions with artificially lit structures

during migration (FLAP Canada 2018). During a seven-year study, van Doren et al. (2017) showed that the intense beams of light projecting skyward at the September 11th memorial site in New York City, USA, attracted and disoriented approximately 1.1 million migrating birds. In response to this finding, the lighting was extinguished during periods of intense migration, which eliminated the negative effect (van Doren et al. 2017).

Not all lights are equally detrimental to birds. Compared to lights that are flashing, lights that are lit continuously appear to impair a bird's ability to determine the distance between itself and a lit structure. Gehring et al. (2009) estimated that 1 to 2 million collisions with brightly lit structures could be avoided if the lights were removed or replaced with red/white flashing lights. The colour of light also affects avian spatial behaviour. Studies analysing avian collisions with aircraft indicate that bird strikes are biased to areas with red lights versus green lights (Dolbeer and Barnes 2017). European Robins (Wiltschko and Wiltschko 2001) and Australian Silvereyes (*Zosterops lateralis*; Wiltschko et al. 1993) alter spatial orientation inside of laboratory enclosures in relation to varying colours of artificial lighting. For example, red light, but not white, green, or blue light, disrupted light-dependent magnetoreception in captive Silvereyes and prevented them from orienting in the seasonally appropriate direction during migration (Wiltschko et al. 1993, Wiltschko and Wiltschko 2001).

In addition to its lethal effects related to collisions, anthropogenic light can have non-lethal effects on avian reproduction. As in many animals, the lengthening day stimulates the development of the avian reproductive system and the expression of sexually selected behaviours, such as singing and mate choice (Tramontin et al. 2001). Artificial night lighting can mimic natural light sources and stimulate similar reproductive events at unnatural times. For example, exposure to anthropogenic night lighting has been associated with earlier reproductive development in European Blackbirds (Dominoni et al. 2013), earlier egg laying and reduced chick mass in Great Tits (de Jong et al. 2015), and earlier singing in Chaffinches (*Fringilla coelebs*), Blue Tits, Great Tits, European Blackbirds, and European Robins (Silva et al. 2014; but see Silva et al. 2017). In Blue Tits, males exposed to artificial lighting also gained twice as many extra-pair copulations as birds that were not exposed to artificial lighting (Kempenaers et al. 2010).

Limitations of Previous Research

There is a growing body of evidence that anthropogenic noise and light affect several facets of avian physiology, behaviour, and ecology. However, there are some limitations to this research. Many studies have been conducted in controlled laboratory settings that carefully and independently control noise and light levels (11 of 44 studies; Table 1.1). Such results may not be applicable to birds living in the wild, where multiple factors interact to shape avian responses to environmental stimuli. In contrast, most field studies are observational in design, with multiple forms of disturbance occurring

simultaneously (27 of 44 studies; Table 1.1). For example, several studies compare birds in urban and rural environments. In these studies, it is often difficult to attribute responses to specific disturbances, since habitat disruption, light pollution, traffic noise, and many other forms of disturbance commonly co-occur in cities (Dominoni et al. 2013, Fuller et al. 2007). Similarly, studies that have examined species in the presence and absence of traffic noise have typically compared birds living along noisy highways to those living in pristine forests away from highways. These studies often detect differences in singing behaviour, but it is unclear whether those differences are due to traffic noise, the lights and pollution associated with traffic, or the highway transecting the birds' natural habitat (Summers et al. 2011). In fact, Summers et al. (2011) showed that the proximity of roadways, not the associated amplitude of traffic noise, was the best correlate of avian species richness and abundance in roadside communities in Ontario, Canada. Likewise, Nenninger and Koper (2018) found that oil infrastructure, not the noise produced by active oil wells, caused the observed 2.5-fold reduction in the number of Baird's Sparrows (*Ammodramus bairdii*) and the 3-fold reduction in the number of Sprague's Pipits (*Anthus spragueii*) in Alberta, Canada. These few studies illustrate the need to study the independent and combined effects of multiple forms of disturbance on birds in their natural environment. An ideal experimental design might use a living laboratory approach, in which the effects of multiple disturbances, such as noise and light, are manipulated independently in a natural environment (Silva et al.

2017). I know of no studies that have manipulated multiple forms of anthropogenic disturbance in a natural environment.

Thesis Objectives

Given the paucity of experimental field studies (Table 1.1), I chose to use an experimental approach within a natural system of free-ranging birds. My study was conducted in a relatively undisturbed boreal forest in the Lake Melville region of Labrador, Canada, approximately 25 km north of the town of Happy Valley-Goose Bay. I used a 2-factor playback experiment to test the independent and combined effects of anthropogenic noise and light on the singing and spatial behaviour of terrestrial free-ranging passerine birds during the 2016 and 2017 avian breeding seasons. Based on previous, primarily correlational, studies, I hypothesized that artificial light would attract birds and that noise would repel them. Additionally, I hypothesized that artificial light would advance the onset of dawn song because it simulates natural light cues available at dawn. I hypothesized that the masking effects of noise would also alter the onset of song, though previous studies have been inconsistent as to whether such noise would advance or delay dawn song (Fuller et al. 2007; Gil et al. 2014; Dominoni et al. 2016). By conducting the experiment in an otherwise undisturbed forest, I avoided the potentially confounding effects of common urban disturbances, including roadways, vehicles, humans, and anthropogenic structures.

Table 1.1. Summary of studies investigating the relationships between anthropogenic noise and light and the singing and spatial behaviour of birds. Studies are ordered chronologically by publication year.

Study	Dependent Variables	Independent Variables	Context	Design
Maillaird 1898	Alteration in flying direction in Fork-tailed Storm Petrels	Presence of fire on beaches	Field	Correlational
Marler et al. 1973	Hearing ability, song structure development, and number of syllables in Zebra Finches	Chronic noise exposure at 90 dB(A) for 40 and 200 days	Laboratory	Experimental
Wiltschko et al. 1993	Spatial orientation of Australian Silvereyes	Presence of four different light colours (white, red, green, blue)	Laboratory	Experimental
Delaney et al. 1999	Frequency of flushing of Mexican Spotted Owl during nesting (fledgling and nesting) and non-nesting seasons; reproductive success (number of young fledged)	Helicopter flight noise and chainsaw noise in relation to increasing distance(s) (<30m to 400m) from site(s)	Field	Correlational
Wiltschko and Wiltschko 2001	Spatial orientation and direction of flight of European Robins	Presence of four light colours (blue, turquoise, green, and yellow) and four brighter variations of the same colours	Laboratory	Experimental
Lohr et al. 2003	Signal-to-noise ratio of detection threshold of budgerigars and Zebra Finch	Signal type in budgerigars, zebra finch, and canary calls; tones, including a pure tone, a tone with frequency modulation, and a tone with amplitude modulation;	Laboratory	Experimental

		Noise, including flat, broad-band noise and low-frequency traffic noise		
Gough et al. 2004	Song minimum frequency, amplitude, syllable length, duration, and individual variation in Pacific Wren songs	Distance to traffic-related noise (80-90 dBa versus ocean-related noise (73 dBa)	Field	Correlational
Quinn et al. 2006.	Vigilance and compensated foraging behaviour (head up position versus head down, number of pecks to ground, peak rate, intake rate) in Chaffinch	Presence of noise (6-8 up to 22.1 kHz) versus novel stimuli	Laboratory	Experimental
Wood and Yezerinac 2006.	Minimum frequency and amplitude of songs in Song Sparrows	Low frequency, high frequency, and amplitude of anthropogenic noise (54.8-71.3 dB)	Field	Correlational
Fuller et al. 2007	Distance of singing birds to urban features, number of birds singing, and number of song phrases	Light levels were measured at 0, 5, 10, 15 and 20 min from the start of the survey period. Ambient noise levels across the day and night	Field	Correlational
Habib et al. 2007	Pairing success and age structure of male Ovenbirds	Chronic industrial noise (75-90 dBa) at compressor sites versus inactive oil well	Field	Correlational
Leonard and Horn 2008	Nestling growth (mean mass and wing chord length) and begging (call length, amplitude, and minimum call frequency)	Experimental placement of 'white' noise playbacks (65 dB) at nest boxes	Field	Experimental

Francis et al. 2009	Nesting species richness, nest predator occupancy, and number of nesting species	Presence/absence of natural gas wells with noise-producing compressors	Field	Experimental
Nemeth and Brumm 2010	Communication distance, vocal pitch, and vocal amplitude of Great Tit and Blackbird songs	Increasing amplitude of traffic noise (45.4-61.1 dB)	Field	Correlational
Bermudez-Cuamatzin et al. 2010	Increase in song frequency, song duration, maximum song frequency, mean length of songs, minimum frequency of song	Exposure to low-amplitude (44-57 dB) and high-amplitude (56-65 dB) urban noise	Laboratory	Experimental
Kempenaers et al. 2010	Laying date, number of extra-pair mates, age class of siring males, proportion of extra-pair young in the brood in Blue Tits Onset of song in Chaffinch, Blue Tit, Great Tit, Blackbird, and European Robin	Presence versus absence of artificial lighting	Field	Correlational
Merkel and Johansen 2011	Light-induced bird collisions in wintering seabirds	Species, frequency, distance from shore, time of collision, visibility conditions	Field	Correlational
Halfwerk et al. 2011b	Song type, switching of song in relation to habitat type, song frequency, song duration	Exposure to urban related noise (100 Hz with decreases at 6.5 dB/kHz) and white noise (1-10kHz)	Field	Experimental
Summers et al. 2011	Species richness	Distance from road Traffic noise level (dB)	Field	Correlational

Arevalo and Newhard 2011	Bird abundance and species richness	Traffic noise level (dB)	Field	Correlational
Halfwerk et al. 2011a	Song types, frequency of song type use, seasonality of low frequency and high frequency songs, female emergence from nest to copulate	Presence of low frequency traffic noise and high frequency traffic noise (gradual increase to 68.0 dB)	Field	Experimental
Hanna et al. 2011	Trill duration, minimum frequency, maximum frequency, energy distribution (25%, 50%, 75% quartiles), entropy, and average frequency in Red-winged Blackbird songs	Experimentally broadcasted silence versus noise and habitat type (roadside versus non-roadside)	Field	Correlational Experimental
Blickley et al. 2012	Lek attendance by male and female Greater Sage-Grouse (pairwise and singles)	Intermittent and continuous drilling and road noise (70 dB(F) from playbacks of energy development	Field	Experimental
McLaughlin and Kunc 2013	Minimum frequency of song, song complexity, song duration, distance to noise source of male European Robins	Increasing traffic noise (70 dB-90 dB)	Field	Experimental
Dominoni et al. 2013	Onset of activity, duration, locomotor activity	Birds captured from urban and rural habitat in lab versus in field	Field-Laboratory	Experimental
Arroyo-Solis et al. 2013	Starting time of singing activity of six bird species: spotless starling, House Sparrow, Eurasian Collared Dove, Greenfinch, Goldfinch, and Serin.	Changes in traffic noise conditions (control versus experimental noise stimulus)	Field	Experimental-Correlational

Silva et al. 2014	Advancement of song in urban European songbirds: European Robin, Common Blackbird, Song Thrush, Great Tit, Blue Tit and Common Chaffinch.	Peaks of car noise (number of vehicles passing on 7 work days), light intensity	Field	Correlational
Cartwright et al. 2014	Duration, minimum frequency, maximum frequency, bandwidth, entropy, number of introductory syllables and timing of Red-winged Blackbird song	Exposure to high traffic noise (>51dB) and low traffic noise (<40 dB) across the week	Field	Correlational
Meillere et al. 2015	Occupancy, laying date, clutch size, and flushing distance of female House Sparrow	Presence/absence of experimental playback of traffic noise at nest boxes	Field	Experimental
Gil et al. 2015	Avian species richness and time of the first song for 10 common bird species	Distance to airport and onset of noise	Field	Correlational
Wiacek et al. 2015	Avian diversity, abundance	Proximity to roadway and related traffic noise (42-81 dB)	Field	Correlational
Potvin et al. 2016	Reproductive success (clutch size, latency to breed number of hatchlings, number of embryo deaths, number of nesting attempts, number of fledglings, and sex ratio.	Exposure to urban related and high frequency noises (40 to 80 dBa, averaging 65 dBa versus silence	Laboratory	Experimental
Long et al. 2016.	Song (changes in minimum frequency), reproductive success and occupancy of Golden-cheeked Warbler	Highway construction noise and related activity noise in a before and after impact assessment	Field	Correlational

Kleist et al. 2016	Song length, number of notes, peak frequency, minimum frequency, maximum frequency, frequency bandwidth, song latency in Spotted Towhees and Chipping Sparrows	Industrial related noise (0-90 dB)	Field	Correlational
Mason et al. 2016	Hunting (success, detection, strike, capture) in Northern Saw-whet Owls	Exposure to increasing noise levels (29-73 dBa)	Laboratory	Experimental
McClure et al. 2016	Age structure (adult versus juvenile), body condition, and capture rate of migrating shorebirds	Exposure to traffic noise (an increase of 6 dBa at 1-3 kHz)	Field	Experimental
Silva et al. 2017	Advancement of the daily onset of birdsong in 14 avian species	Illumination of a naturally darkened forest edge with street lamps (white, green, and red colours) from sunset to sunrise	Field	Experimental
Swaddle and Ingrassia 2017	Flight behaviour (deacceleration, flight velocity, body posture, and collision with mist net) of 18 adult Zebra Finches	Mist-net with and without presence of noise	Laboratory	Experimental
van Doren et al. 2017	Radar observations of peak bird density and maximum number of birds detected within 500 m of an installation during lit and unlit periods	Presence of intense urban lighting during lit and unlit periods	Field	Correlational

LaZerte et al. 2017	Increase in song frequency and variability of calls versus song in Mountain Chickadee	Five-minute traffic noise playbacks and ambient traffic noise	Field	Experimental
Derryberry et al. 2017	Changes in song minimum frequency and amplitude	Exposure to traffic noise (<25 to >40 dB)	Field	Correlational
Dolbeer and Barnes 2017	Bird collision	Aircraft wing light colour/ placement on aircraft (left/red versus right/green) across the day	Field	Correlational
Buxton et al. 2017	Disturbance behaviour (vigilance, flying, wing fluttering) during incubation period, chick-rearing period with Gull presence	Park visitor related noises (high, low)	Field	Correlational
Nenninger and Koper 2018	Species relative abundance and occupancy: Sprague's Pipit, Baird's Sparrow, Western Meadowlark, Savannah Sparrow, Chestnut-collared Longspur	Presence/absence of oil infrastructure, infrastructure type, and presence/absence of oil industrial related noise	Field	Experimental

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Co-authorship Statement

Any manuscript derived from chapter 2 will include as co-authors David Wilson and Jeffrey Ethier. DW supervised all aspects of the project, contributed to experimental design and statistical analysis, and provided financial support. JE assisted with field work, data extraction, and statistical analysis. The overall project was the responsibility of Bronwen Hennigar, as per the partial requirements of a Master of Science thesis in the Cognitive and Behavioural Ecology program at Memorial University. Chapter 2 is prepared as a manuscript for submission to the journal *Behavioural Ecology*, so necessarily includes some overlap with the general introduction and discussion.

Chapter 2: Traffic Noise Attracts Birds During the Breeding Season

Abstract

Understanding the effects of anthropogenic disturbance on animal behaviour is challenging because multiple forms of disturbance often co-occur. Observational studies measure the combined effects of multiple disturbances, such as traffic noise, artificial lighting, and habitat alteration within urban habitats. Experimental manipulations on captive animals can disentangle these effects, but often omit important ecological factors and may not translate to animals living in the wild. I tested the effects of traffic noise and anthropogenic light on the vocal and spatial behaviour of wild birds of the order Passeriformes during the 2016 and 2017 avian breeding seasons in undisturbed boreal forest habitat in Labrador, Canada. I manipulated the presence and absence of traffic noise and light at 110 locations. Each treatment was surrounded by an 8-channel microphone array that recorded and localized avian vocalizations throughout the manipulation. I examined the independent and combined effects of noise and light on the timing of the first vocalizations of the dawn chorus and the proximity of the vocalizing birds to the disturbance. I analyzed all species combined, and then conducted separate analyses for the six most common species: Boreal Chickadee, Dark-eyed Junco, Ruby-crowned Kinglet, Swainson's Thrush, White-throated Sparrow, and Yellow-rumped Warbler. When all species were analyzed together, vocalizing birds were attracted to noise. There was some evidence that light repelled birds and caused them to vocalize

earlier, but this evidence was inconsistent. Species-specific analyses produced similar results to the global passerine analysis. My study provides some of the first experimental evidence of the independent and combined effects of traffic noise and light on the vocal and spatial behaviour of wild birds, and suggests that breeding birds may be attracted to noisy roads where they would be exposed to additional forms of disturbance.

Introduction

Urban and industrial developments produce multiple anthropogenic disturbances that negatively impact wildlife (Smit and Visser 1993). Some, such as chemical contamination and anthropogenic structures, kill animals quickly and directly (Harrison et al. 1997; Wilcox et al. 2016; Bernardino et al. 2018; Green et al. 2018), but others have more subtle and prolonged effects that can be difficult to detect. In the last century, anthropogenic noise and light from cities, roadways, and industry have been recognized as widespread forms of disturbance that affect the physiology, ecology, and behaviour of animals (Blickley and Patricelli 2010; Ortega 2012). Although all animals are at risk, birds may be especially vulnerable to noise and light because they frequent noisy and illuminated areas (Marzluff 2014) and rely heavily on acoustic communication (Slabbekoorn and Peet 2003; Slabbekoorn and Ripmeester 2008).

Birds exposed to anthropogenic noise can experience several adverse effects. They can incur physical damage, including brain deformities, hearing loss, and deafness (Marler et al. 1973), cognitive impairments, including learning and memory deficits (Potvin et al. 2016), and physiological stress, including rapid heart rate and elevated stress hormones (Kleist et al. 2018). Noise can also alter a bird's behavioural ecology by interfering with acoustic communication (Ortega 2012). For example, noise can interfere with predator avoidance by masking predator cues and conspecific alarm calls (Francis et al. 2009; Mason et al. 2016), and with reproductive behaviour by masking or altering

sexually selected acoustic displays (Slabbekoorn and Peet 2003; Halfwerk et al. 2011a; Aunay et al. 2014). The effects of noise on song are especially well-documented, with several studies showing that high-energy, low-frequency noise, such as traffic noise, causes birds to shift the timing of song production (Fuller et al. 2007; Cartwright et al. 2014; Gil et al. 2015; Dominoni et al. 2016) and to alter the structure of individual songs in ways that are thought to minimize masking. For example, birds living in noisy environments are known to shift song production to quieter parts of the day and to increase the amplitude (Brumm 2004), minimum frequency (Bermudez-Cuamatzin et al. 2010), tonality (Hanna et al. 2011), and duration (Gentry et al. 2017) of their songs. In some cases, birds might avoid noisy, but otherwise ideal, habitats in favour of habitats that are suboptimal in other respects (Bayne et al. 2008; Potvin 2017). It is also possible that birds may not be able to avoid noise because of its pervasiveness in most ecosystems, including in naturally protected areas (Shannon et al. 2016).

Like noise, anthropogenic light can have adverse effects on birds (Longcore and Rich 2004). Artificial lighting can impact sleep and circadian rhythms (Longcore and Rich 2004; Ouyang et al. 2017), which can alter the timing of critical activities (Tramontin et al. 2001; Dominoni et al. 2013; Silva et al. 2017). For example, Kempenaers et al. (2010) and Dominoni et al. (2013) showed that artificial lighting causes birds to initiate reproduction earlier in the breeding season by inducing them to develop reproductive organs up to a month earlier, molt earlier, and advance the onset of egg laying. Light can

also affect the spatial ecology of birds. For example, seabirds (Wilhelm et al. 2013; Rodriguez et al. 2017) and migrating songbirds (van Doren et al. 2017) approach artificial lighting, which can increase their risk of predation (Canario et al. 2012) and collision (Fortin and Andruskiw 2003; Montevecchi 2006; Lesmerises et al. 2018). In North America, collisions with artificially lit structures are thought to kill between 100 million and 1 billion birds per year (FLAP 2018).

Understanding the effects of anthropogenic noise and light on birds is challenging because noise, light, and the structures that produce them (*e.g.*, cities, roadways, industry) often co-occur. Some studies compare disturbed populations living near cities, airports, or highways to populations in areas of minimal disturbance (Seger-Fullam et al. 2012; Dominoni et al. 2013; LaZerte et al. 2015). However, cities, highways, and airports combine habitat alteration, noise, light, and chemical pollution, and altered biological community compositions, so ascertaining the independent effects of noise and light, or any other specific form of disturbance, has proven difficult (Summers et al. 2011; Gentry et al. 2018; Nenninger and Koper 2018). Laboratory experiments on captive animals can disentangle the effects, but often omit important ecological factors and may not translate to animals living in the wild (Wiltschko and Wiltschko 2001; Swaddle and Ingrassia 2017). Consequently, there is a need to conduct experimental manipulations on wild birds to fully understand how anthropogenic noise and light affect their behaviour.

In this study, I manipulated the presence of anthropogenic noise and light to better understand their independent and combined effects on the singing and spatial behaviour of wild birds. I focused on the order Passeriformes because passerines are primarily diurnal and thus vulnerable to the effects of nocturnal lighting. They also rely heavily on vocal communication for attracting mates, repelling rivals, and coordinating activities with offspring and other conspecifics (Bateson and Feenders 2010).

Based on previous studies, I made several predictions about how birds would respond to experimental noise and light. First, I predicted that traffic noise would cause birds to distribute their vocalizations more evenly throughout the day (Fuller et al. 2007; Cartwright et al. 2014) and, therefore, to be heard earlier in the morning, as compared to birds living in quiet areas that would concentrate their songs within a defined dawn chorus. In support of this prediction, Fuller et al. (2007) found that European Robins sang more songs at night when occupying urban habitats that were noisy versus quiet during the day. Additionally, Fuller et al. (2007) found that the presence of anthropogenic noise, rather than the presence of artificial light, was the primary predictor of the onset of birdsong when both types of disturbance were considered within the study. Likewise, Cartwright et al. (2014) showed that birds living along noisy highways distributed their songs more evenly throughout the day, whereas birds living in quiet rural areas concentrated their songs during brief dawn and dusk choruses.

Second, I predicted that noise would repel birds. Summers et al. (2011) found that species richness increased as the distance from the road increased and the amplitude of the associated traffic noise decreased, suggesting that birds avoid noisy roadways. Third, I predicted that experimentally produced night lighting would attract birds, as has been shown for Balearic Shearwater (*Puffinus mauretanicusI*), Scopoli's Shearwater (*Calonectris diomedea*), and European Storm-petrel (*Hydrobates pelagicus*; Rodriguez et al. 2015). Other studies have found that several passerine species are likewise attracted to artificial light, including offshore and urban lighting (Montevecchi 2006), experimentally produced green light (Poot et al. 2008), lighthouses (Jones and Francis 2003), and television towers lit with red and white lights (Cochran and Graber 1958). Fourth, I predicted that experimentally produced night light would cause birds to sing earlier. American Robin (*Turdus migratorius*; Miller 2006), Blue Tit (*Cyanistes caeruleus*; Kempenaers et al. 2010; Da Silva et al. 2015), European Robin (*Erithacus rubecula*), Common Blackbird (*Turdus merula*), Great Tit (*Parus major*), Song Thrush (*Turdus philomelos*), and Common Chaffinch (*Fringilla coelebs*) have all been shown to sing earlier in the presence of artificially produced light, as compared to birds exposed only to natural light (Da Silva et al. 2015). Finally, by combining the evidence for the independent effects of artificial noise and light, I predicted that birds in the presence of artificial noise and light would be heard even earlier than when only noise or light were present, and that the repellent effects of noise would offset the attractive effects of light.

Methods

Study Area

I conducted 110 trials during the 2016 (68 trials) and 2017 (42 trials) avian breeding seasons (16 May to 10 July). Trials were distributed across an approximately 50 x 50 km area near Happy Valley-Goose Bay, Labrador, Canada (Figure 2.1). Black Spruce (*Picea mariana*) and Balsam Fir (*Abies balsamea*) were the dominant tree species at my trial locations, though other species were present, including Tamarack (*Larix laricina*), White Birch (*Betula papyrifera*), Heart-shaped Birch (*Betula cordifolia*), and Trembling Aspen (*Populus tremuloides*). Vegetative species included Speckled Alder (*Alnus incana*), American Mountain-ash (*Sorbus americana*), Squashberry (*Viburnum edule*), Willow species (designated as *Salix* spp.), Serviceberry (*Amelanchier* spp.), and Skunk Currant (*Ribes glandulosum*). The most common ericaceous understory species were Bog Labrador Tea (*Rhododendron groenlandicum*), Sheep Laurel (*Kalmia angustifolia*), Swamp Laurel (*Kalmia polifolia*), and Leatherleaf (*Chamaedaphne calyculata*).

Within the study area, trial locations were selected at random, but with the constraints that they were between 0.5 km and 1 km from road access, not in a swamp or body of water, and a minimum distance of 0.5 km from other trial locations. As part of another study (Ethier, unpublished data), 20 trial locations used in 2016 were re-used in new trials in 2017. I consider these trials as independent replicates because they

involved different treatments in each year and because there was high species turnover at each site between years (Ethier, unpublished data).

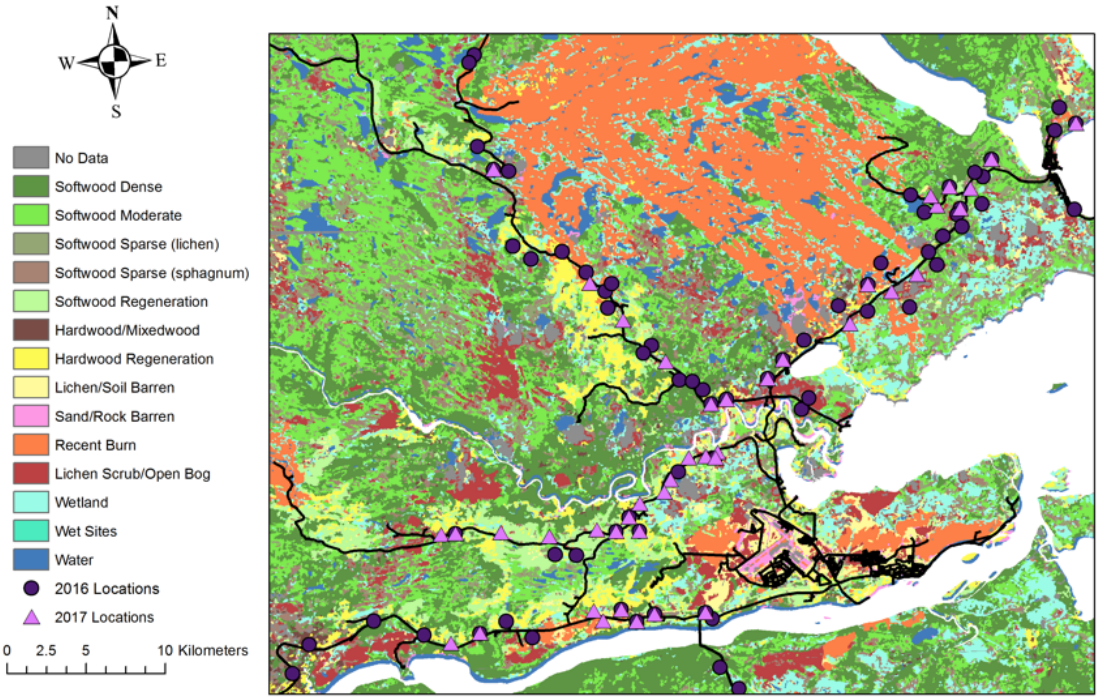

Figure 2.1 Map of the 110 trial locations and their associated habitat types at my study area near Happy Valley-Goose Bay and North West River, Labrador, Canada. Trials were conducted during the 2016 (n = 68, depicted by circles) and 2017 (n = 42, depicted by triangles) avian breeding seasons (May-July). Base map provided by Nature Conservancy of Canada and Memorial University of Newfoundland. Original figure is in colour.

Microphone Arrays

At each trial location, I set up an 8-channel microphone array that allowed me to record and localize avian vocalizations throughout the trial. Each array consisted of four

digital audio recorders (Model: SM3; Wildlife Acoustics, Concord, MA, USA) attached to trees, approximately 1.5 m above the ground, at the four corners of an approximately 40 x 40 m square. Each recorder had two microphones: one that was built into the recorder (omnidirectional pickup pattern; 50–20000 Hz (± 10 dB) frequency response; Wildlife Acoustics, Concord, MA, USA) and a second, external microphone (model: SMM-A2; omnidirectional pickup pattern; 50–20000 Hz (± 10 dB) frequency response) that was positioned in the forest canopy approximately 2 m above the first. I elevated the external microphone with an extendable painter's pole and fixed it in place by hooking a wire attached to the microphone over a tree branch. The microphones were pointed towards the centre of the array, and their locations determined with a survey grade global navigation satellite system (GNSS) with 10-cm accuracy (model: Trimble Geo 7X; Trimble Inc., Sunnyvale, CA, USA). As a requirement for acoustic localization, the clocks of the four audio recorders were synchronized to within 1 ms of each other by connecting them to external GPS units (model: Garmin SM3 GPS; Wildlife Acoustics, Concord, MA, USA) for the duration of the trial (Mennill et al. 2012).

Audio recorders were programmed to record continuously until manually stopped, creating a new stereo audio file every 2 h (WAVE format, 24 kHz sampling rate, 16-bit amplitude encoding, 220 Hz analog high-pass filter, 10 dB analog voltage gain). I had four microphone arrays in 2016, and, on average, was able to set up two arrays at new locations each day. In 2017, I had two microphone arrays, with one being set up at

a new location each day. Arrays were set up in the afternoon and were left recording for a minimum of 48 h. The first 24 h was used as part of another study (Ethier, unpublished data) and did not involve any manipulations. The next 24 h served as an experimental period in which I recorded singing behaviour during and after experimental disturbance treatments were broadcast.

I set up a Kestrel 5500 portable weather station (Kestrel Meters, Boothwyn, PA, USA) inside each array to record a suite of weather variables at 20-min intervals, including temperature (± 0.1°C), wind speed (± 0.1 km/h), relative humidity (± 0.1%), and barometric pressure (± 0.1 mb). Temperature influences the speed of sound, which is required for the sound localization process. Wind can also influence the likelihood of detecting signals on recordings. However, windspeed within my microphone arrays was always low (mean = 0.75 km/h, sd = 1.65 km/h), so was not considered further. Humidity and barometric pressure were not considered in subsequent analyses because they have been found previously to have negligible effects on signal detection and localization (Wölfel and McDonough 2009).

Disturbance Treatments

I returned to the microphone array before 1700 h on the day after it was set up and installed one of four disturbance treatments: (1) no light and no noise (*i.e.*, control; *N* = 39); (2) light but no noise (*N* = 35); (3) noise but no light (*N* = 17); or (4) noise and

light (*N* = 19; Appendix 1). Treatments were selected at random, but with the constraint that the speaker used to broadcast noise could only be used every second day due to the time needed to recharge its internal battery. Due to this limitation, the sample sizes for treatments involving noise were smaller than the sample sizes for other treatments.

The noise treatment was broadcast from an amplified loudspeaker (model: SBT1009BK; woofer diameter: 20.32 cm; tweeter diameter: 7.62 cm; The Sharper Image, Farmington Hills, MI, USA) placed facing upwards in the centre of the array. The speaker was connected to an external lithium ion battery (model: Car Rover B019DVZXTE; 26 amp-hour; 12-V; Startwayauto Store, Guangzhou, Guangdong, China) that supplemented its internal battery, and to a digital audio player (model: HS-636-4GBBK MP3 Player; Hipstreet, Markham, ON, Canada) that played the noise stimulus. The entire apparatus was sealed inside a black plastic bag to protect it from rain. The noise stimulus was programmed to begin playing at 1700 h (*i.e.*, ca. 24 h after the array was set up) and to continue for 15 h (*i.e.,* until 0800 h the following morning.

The noise treatment included three noise stimuli, which, together, represented a range of traffic types. The stimuli were derived from online sources and were assigned at random to trials involving a noise treatment. They varied primarily in terms of the rates of traffic they contained. The first stimulus was recorded from a country highway and was 1 h in length (Soundjay.com 2016), with approximately seven vehicles passing per

minute. The second stimulus was recorded from a two-lane highway (Soundjay.com 2016), with approximately 10 vehicles passing per minute, and was 8 h in length. The third noise stimulus was recorded from a busy freeway, with approximately 40 vehicles passing per minute, and was 8 h in length (Highway Sounds, White Noise, Youtube 2014). Using Audacity recording and editing software (version 2.0; Audacity® software is copyright © 1999–2018 Audacity Team; the name Audacity® is a registered trademark of Dominic Mazzoni), each stimulus was normalized to a peak amplitude of -1 dB and then repeated to construct a 15-h playback sequence. The three traffic noise stimuli were assigned at random to trials involving noise.

During playback in the field, I set the volume on the speaker and the digital audio player to 'maximum' to ensure that all stimuli played at approximately the same amplitude in different trials. Using a digital sound level meter (model 33-2055; C weighting; fast response; RadioShack Corporation, Fort Worth, TX, USA), I measured the peak amplitude of each stimulus over a 5-min period at six predetermined distances from the speaker (1, 5, 10, 15, 20, and 25 m; Table 2.1). These measurements were taken at the beginning of six trials in 2016, when the speaker’s batteries were fully charged.

Table 2.1. Peak sound pressure level of the noise stimuli at 6 different distances from the speaker. Sound pressure level (SPL) was measured in decibels at 6 array sites with a digital sound level meter (C-weighting, fast response; effective range: 50–126 dB SPL) over a 5-min period.

Distance from speaker (m)	Average (dB)	Standard Deviation (dB)	Minimum (dB)	Maximum (dB)
1	84.8	2.8	82	88
5	70.3	9.5	62	84
10	61.5	8.1	55	73
15	54.3	3.9	50	58
20	50.5	1.2	50	52
25	< 50.0	0.0	< 50	50

The light treatment was a battery powered light emitting diode (LED; Super Bright LEDs Inc., St. Louis, MO, USA) that was hung by its power cable from a tree branch at an average height of 4.3 m above the ground (SD: 0.8 m; range: 2.6–5.7 m) in the centre of the array. At this height, the light's 40° beam angle provided an average area of ground illumination of 7.8 m^2 (SD: 2.9 m^2; range: 2.7–13.5 m^2). The light was connected to a light-sensitive switch (model: GLUX-DDS Dusk-to-Dawn Sensor; Super Bright LEDs Inc., St. Louis, Missouri, U.S.A) that activated the light at approximately sunset and deactivated the light at approximately sunrise. At the time and location of my study, the average sunset occurred at 2122 h (range: 2057–2133 h) and the average sunrise occurred at 0440 h (range: 0433–0459 h; timeanddate.com, 2018). In trials involving noise and light treatments, I attempted to hang the light directly above the speaker, though vegetation and topography sometimes required them to be separated slightly (average ± SD horizontal distance: 2.7 ± 2.2 m). I chose to use LEDs, as opposed to other types of exterior lighting, because LEDs are energy efficient, long-lasting, available in diverse colours, and increasing in popularity (Mottier 2009).

For each trial involving a light treatment, I randomly selected one of five different LED colours that are commonly used in exterior lighting and which wild birds might encounter: red (model: GLUX-RGB18W-S40B-MCL; colour: 622 nm; power: 6 W; Super Bright LEDs Inc., St. Louis, MO, USA), green (model GLUX-RGB18W-S40B-MCL; colour: 528 nm; power: 6 W), blue (model GLUX-RGB18W-S40B-MCL; colour: 474 nm; power: 6

W), cool white (model GLUX-CW6W-S40; correlated colour temperature: 5800 °K; power: 6 W), and warm white (model GLUX-WW6W-S40B; correlated colour temperature: 3100 °K; power: 6 W). Although white lights (warm or cool white) would be the most frequently encountered by passerine birds, exposure to other colours would also likely occur, so including multiple light colours ensures that my stimuli represent diverse forms of light disturbance.

Acoustic Analysis

For each 2-h interval of a trial, I used Audacity software to combine the set of four stereo audio files that had been recorded simultaneously by the array into a single 2-h, 8-channel sound file (WAVE format; 16-bit amplitude encoding; 24 kHz sampling rate). The 8-channel file was named according to the array number, date, and start time of the recording. Using Audacity, I then viewed as spectrograms (512-point fast Fourier transformation (FFT), 87.5% overlap, Hamming window) all 8-channel audio files recorded between midnight and 0800 h on the night when the treatments were deployed. During the data scoring process, I remained blind to the disturbance treatment being broadcast. Whenever I detected a vocalization from a passerine (see representative spectrograms from each species in Appendix 2), I marked the time of its onset and offset and annotated it according to species, which I defined according to the online Checklist of North and Middle American Birds (Table 2.2; Chesser et al. 2018). For most species, I annotated their species-specific songs, but, for Boreal Chickadee, Red-

breasted Nuthatch, and Common Raven, which do not produce songs, I annotated their species-specific calls (Rodewald 2015). I included vocalizations only if they were visible on the audio channels corresponding to at least three of the four corners of the array, since vocalizations can only be localized when they are detected at three or more locations in an array (Mennill et al. 2012; Wilson et al. 2014). Based on our previous experience with this array configuration, songs detected by one or two recorders only originate from at least 40 m away from the centre of the array (personal observation; Wilson et al. 2014). Finally, I annotated only the first 10 songs produced after midnight from each species, or all of the songs from a species if it produced fewer than 10 songs. In total, I annotated 7907 vocalizations from 31 passerine species (Table 2.2).

Table 2.2 Avian vocalizations included in this study. The column "vocalizations detected" shows the number of arrays in which a species was detected from among the 110 array locations, and, in parentheses, the number of vocalizations detected from that species across all arrays. Vocalizations were considered 'detected' if they were visible on the spectrograms corresponding to three of the four corners of the array (see text for details). For my study, I annotated a maximum of 10 vocalizations per species per array. The column "vocalizations within 30 m" shows the same information, but based on the subset of vocalizations that were localized to within 30 m of the experimental disturbance (or of the centre of the array for control trials) with a localization error of 0.02 or less (see text for explanation of this error term). The six species that were present in the greatest number of arrays, as defined by the column ‘vocalizations within 30 m’, were also analyzed individually and are shown in bold. The column "passerine analysis" shows the same information again, but based on the subset of songs that composed the two response variables included in the final statistical analysis of all passerines combined (see text for details). The passerine analysis is based on the first five songs produced by any passerine after midnight, so necessarily excludes songs that otherwise met the inclusion criteria. The final column shows the bandpass filter settings used for each species during the localization procedure.

common name	scientific name	vocalizations detected	vocalizations within 30 m	passerine analysis	bandpass filter (Hz)
Alder Flycatcher	*Empidonax alnorum*	10 (82)	2 (11)	1 (1)	2387–6594
American Redstart	*Setophaga ruticilla*	1 (7)	0 (0)	0 (0)	3729–9013
American Robin	*Turdus migratorius*	55 (490)	13 (44)	5 (15)	1760–4969
Black-throated Green Warbler	*Setophaga virens*	37 (296)	12 (35)	6 (11)	3042–6470
Blackpoll Warbler	*Setophaga striata*	1 (10)	1 (1)	0 (0)	4008–9223
Boreal Chickadee	***Poecile hudsonicus***	**58 (455)**	**20 (84)**	**11 (23)**	**3348–8336**
Brown Creeper	*Certhia americana*	8 (49)	2 (3)	0 (0)	3878–7309
Cape May Warbler	*Setophaga tigrina*	15 (122)	2 (6)	2 (6)	3545–9291
Common Raven	*Corvus corax*	7 (52)	1 (1)	1 (1)	931–1875
Common Redpoll	*Acanthis flammea*	6 (39)	3 (4)	2 (3)	2830–6650
Connecticut Warbler	*Oporornis agilis*	1 (10)	0 (0)	0 (0)	3090–6040
Dark-eyed Junco	***Junco hyemalis***	**88 (816)**	**36 (221)**	**24 (72)**	**2975–6839**
Fox Sparrow	*Passerella iliaca*	78 (713)	16 (51)	8 (14)	2134–5774

Golden-crowned Kinglet	*Regulus satrapa*	1 (1)	0 (0)	0 (0)	6840–8250
Hermit Thrush	*Catharus guttatus*	47 (427)	7 (12)	4 (5)	2347–5308
Lincoln's Sparrow	*Melospiza lincolnii*	29 (198)	15 (57)	14 (38)	1557–7204
Magnolia Warbler	*Setophaga magnolia*	9 (77)	4 (15)	1 (3)	2460–8032
Northern Waterthrush	*Parkesia noveboracensis*	15 (110)	4 (25)	3 (12)	2196–7672
Orange-crowned Warbler	*Oreothlypis celata*	28 (222)	11 (34)	3 (6)	2451–8544
Palm Warbler	*Setophaga palmarum*	1 (10)	1 (4)	1 (4)	4500–8000
Philadelphia Warbler	*Vireo philadelphicus*	2 (13)	0 (0)	0 (0)	1600–6200
Pine Grosbeak	*Pinicola enucleator*	30 (225)	8 (25)	3 (6)	2085–5223
Pine Siskin	*Spinus pinus*	38 (311)	15 (49)	5 (10)	3665–6875
Red-breasted Nuthatch	*Sitta canadensis*	15 (92)	5 (10)	0 (0)	1046–6844
Ruby-crowned Kinglet	***Regulus calendula***	**79 (713)**	**31 (130)**	**13 (31)**	**1982–6518**
Swainson's Thrush	***Catharus ustulatus***	**71 (702)**	**26 (124)**	**20 (63)**	**1630–5503**
Tennessee Warbler	*Oreothlypis peregrina*	22 (214)	10 (37)	6 (11)	2533–9993

White-throated Sparrow	***Zonotrichia albicollis***	**80 (702)**	**20 (48)**	**16 (30)**	**2235–7130**
Winter Wren	*Troglodytes hiemalis*	7 (62)	3 (10)	2 (4)	2579–9491
Yellow-bellied Flycatcher	*Empidonax flaviventris*	2 (20)	1 (6)	0 (0)	2761–5994
Yellow-rumped Warbler	***Setophaga coronata***	**79 (667)**	**38 (163)**	**16 (39)**	**2827–6520**

Vocalizations were localized automatically using a custom program in MATLAB (Version 6.1, The MathWorks, Natick, MA, USA). For each vocalization, the program uses information about its position within the parent file to open the 8-channel clip containing the vocalization. The program applies a species-specific high-pass filter to remove low-frequency background noise (Table 2.2). It then identifies the channel with the highest signal-to-noise ratio and uses waveform cross-correlation to measure the time-of-arrival differences of the signal between that channel and the other seven channels in the array. The program then simulates a 3-dimensional lattice over the study area, and, for each vertex in the lattice, calculates how long it would take for a sound to reach each microphone in the array, as well as the corresponding time-of-arrival differences among the microphones. For each vertex, the sum of the absolute differences between the theoretical and observed time-of-arrival differences are calculated and used as a unitless measure of localization error. Localization error is a measure of model fit, not a measure of geographic distance. The vertex that minimizes localization error is selected as the best estimate of the origin of the sound.

Vocalizations were removed from further analysis if their localization error value was greater than 0.02. Previous research involving the playback of sounds from known locations within my arrays (but after my trials were complete) showed that 90% of localizations with an error value of 0.02 or less were within 3.6 m of their true locations, as determined by our GNSS (Ethier, unpublished data). For each remaining vocalization, I

calculated the distance between its estimated origin and the experimental disturbance using the R packages 'sp' (Bivand et al. 2013) and 'rgeos' (Bivand and Rundel 2018). If both a light and speaker were present, I calculated the distance to the midpoint between them, and, if the speaker and light were both absent, I calculated the distance to the centre of the array. I excluded from further analysis any vocalizations that were more than 30 m away from the disturbance, or, for control trials, from the centre of the array. A 30-m radius around the disturbance ensured that vocalizations originated from locations within or close to the array, where noise and light treatments could be detected by human observers (personal observation; Table 2.1). Beyond 30 m, I often could not detect noise and light treatments, suggesting that birds may also have been unable to detect them at such distances. Of the 7907 vocalizations from 44 avian taxa that I originally annotated, 1470 vocalizations from 31 species (see representative spectrograms in Appendix 2) and 89 trials were localized to within 30 m of the disturbance (or the centre of array for control trials) with a localization error of 0.02 or less (Table 2.2). In 21 trials, no target species met the inclusion criteria, so these trials were excluded from statistical analyses. The dependent variables used in statistical analyses were derived from this final dataset.

Statistical Analysis

I expected any effects of noise and light to be most evident early in the morning, when most birds begin to sing (Leopold and Eynon 1961; Thomas et al. 2002). If birds

advance the onset of song in response to light, then that effect should be most evident when birds first start to sing. For each trial, I identified the first five vocalizations produced after midnight by any passerine, as well as the first five vocalizations produced after midnight by each passerine species. My rationale for including the first five vocalizations, rather than the first vocalization only, was that birds sometimes produce isolated songs at night that do not reflect the general onset of the individual's dawn chorus (Leopold and Eynon 1961). For all species combined, and separately for each species, I calculated the average time of the first five vocalizations (number of seconds after midnight, followed by conversion to minutes) and the average 2-dimensional Euclidean distance between the origin of the first five vocalizations and the experimental disturbance. If the trial included a light and speaker that were slightly separated, I calculated distances to the midpoint between the light and speaker. For control trials (*i.e.*, no noise and no light), distances were calculated relative to the centre of the array. Average time and average distance to disturbance for the first five vocalizations were used as dependent variables in subsequent statistical analyses.

I used 2-factor ANOVAs to test for the effects of noise (present versus absent), light (present versus absent), and the two-way interaction between noise and light on each dependent variable. I analyzed all birds combined, and then conducted species-specific analyses for the six most common species, as determined by the proportion of arrays in which they were localized to within 30 m of the disturbance with a localization

error of 0.02 or less (Table 2.2). These included: Boreal Chickadee, Dark-eyed Junco, Ruby-crowned Kinglet, Swainson's Thrush, White-throated Sparrow, and Yellow-rumped Warbler. Each of these species was detected within 30 m of the stimulus (or the centre of the array for control trials) with a localization error of 0.02 or less in at least 20 arrays (*i.e.,* an average of at least 5 arrays per treatment). The next most common species, Fox Sparrow, was present in only 16 arrays (Table 2.2). All analyses met the assumptions of ANOVA, including normally distributed residuals, homogeneity of variance, and independence among observations.

I included five different colours of light in my light treatment to ensure that my stimuli were representative of the broad category of light disturbance, and to permit a preliminary investigation into the effects of light colour on avian responses. Previous research has shown that birds respond differently to different colours of light (Poot et al. 2008; Wiltschko and Wiltschko 2001; Dolbeer and Barnes 2017), so it is possible that responses to one colour could have offset responses to another in my general analysis of treatment effects. For example, birds might have been attracted to red lights, but repelled by green lights. I therefore conducted additional analyses to determine if either of my two response variables were influenced by light colour. For the subset of 73 trials that did not involve a noise playback, I compared each response variable from the passerine dataset among the six light conditions using 1-factor ANOVA. Note that sample sizes among treatment groups were variable and, for some colours, quite small

(no light N = 38, cool white N = 8, warm white N = 6, red N = 9, green N = 7, blue N = 5), so results should be interpreted with caution.

Results

Passerine Analysis

When all passerine species were analyzed together, the average time of the first five vocalizations was 0434 h ± 72 min (mean ± SD; Figure 2.2). For reference, sunrise at the time and location of my study occurred at 0440 h ± 7.31 min (mean ± SD; range: 0433–0459 h; timeanddate.com, 2018). The average time of the first five vocalizations was not affected by the presence or absence of experimental noise or light (2-factor ANOVA: $F_{3,85}$ = 0.29, p = 0.832; Figure 2.2; Appendix 3).

The average distance to disturbance during the first five vocalizations was 17.6 ± 7.0 m (mean ± SD; Figure 2.3). There was a statistically significant effect of treatment on distance (2-factor ANOVA: $F_{3,85}$ = 14.05, p < 0.001), with birds being attracted to noise (coefficients analysis: t = -5.64, p < 0.001; Figure 2.3; Appendix 3). There was no effect of light (t = 0.09, p = 0.929) or the interaction between noise and light (t = 1.77, p = 0.081) on the average distance to disturbance (Figure 2.3; Appendix 3).

The colour of light did not affect the average time of the first five vocalizations (1-factor ANOVA: $F_{5,51}$ = 1.24, p = 0.304; Figure 2.4), but it did affect the average distance

to disturbance during the first five vocalizations ($F_{5,51}$ = 2.68, p = 0.032), with birds being significantly attracted to blue light relative to no light (coefficients analysis: t = -2.49, p = 0.016). Birds were not affected by any of the other colours of light, relative to the no-light condition (all $|t| < 1.45$, all $p > 0.15$; Figure 2.4).

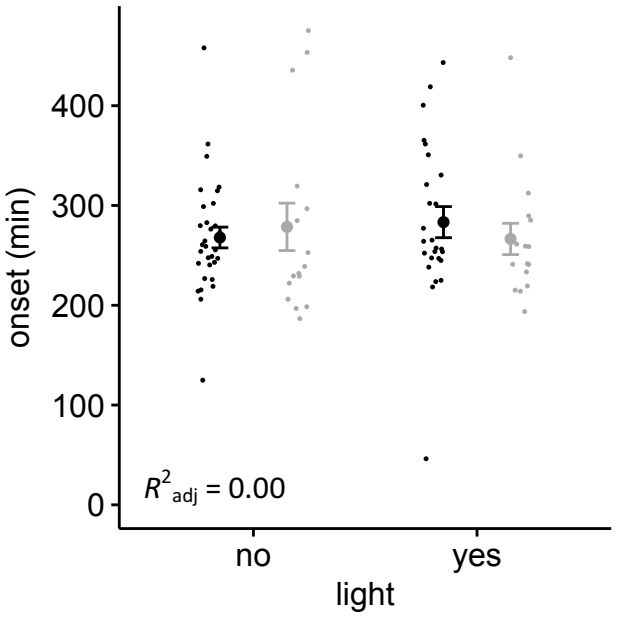

Figure 2.2 The effects of noise (noise absent = black; noise present = grey), light, and the interaction between noise and light on the average time (number of minutes past midnight) of the first five vocalizations produced by any passerine (N = 89 trials). Large dots and error bars show mean ± SD. Small dots show the average time of onset for the first five songs of a given trial.

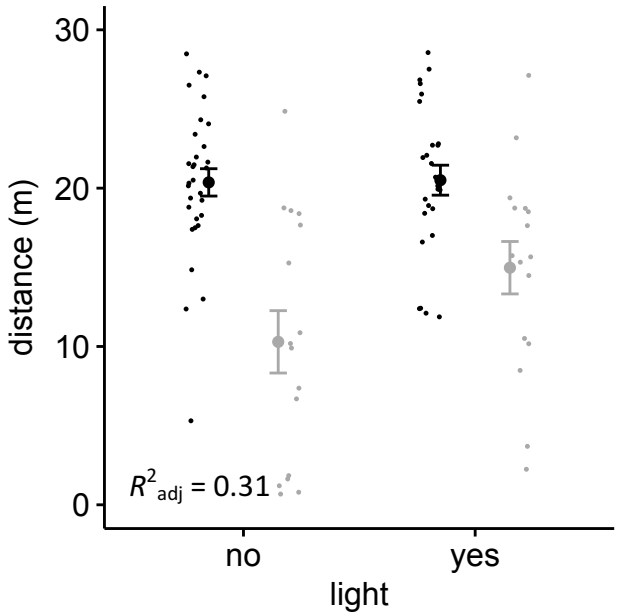

Figure 2.3 The effects of noise (noise absent = black; noise present = grey), light, and the interaction between noise and light on the average distance to disturbance (or distance to the centre of the array for control trials) of the first five vocalizations produced by any passerine (*N* = 89 trials). Large dots and error bars show mean ± SD. Small dots show the average distance to disturbance of the first five songs of a given trial.

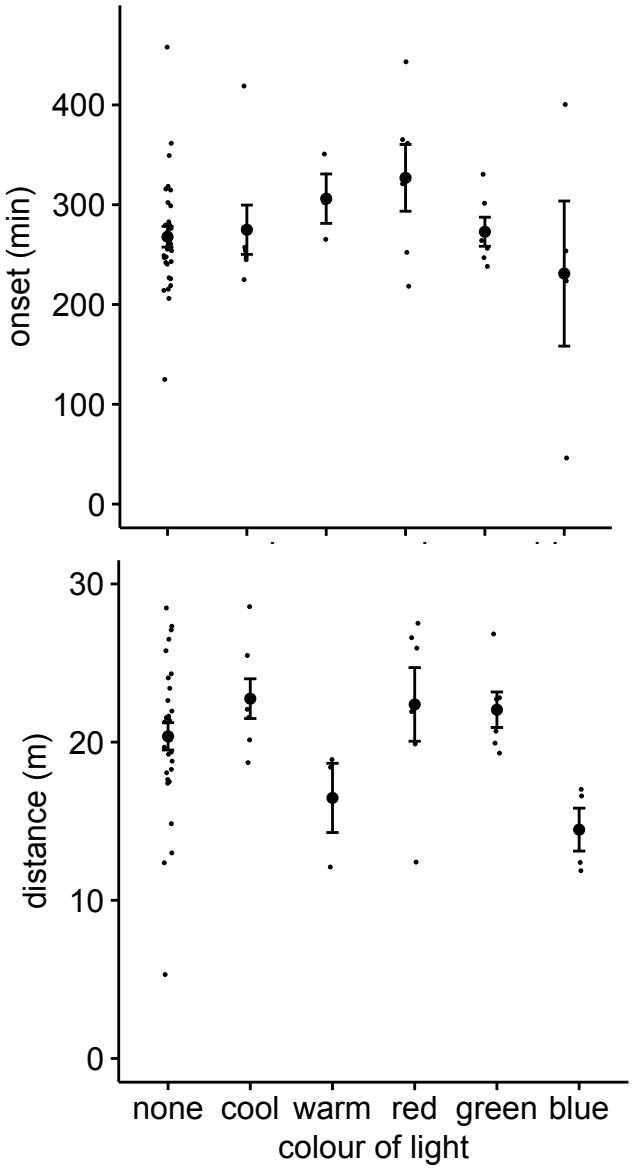

Figure 2.4 The effects of light colour on the (a) average time (number of minutes past midnight) and (b) average distance to disturbance (or distance to the centre of the array for control trials) of the first five vocalizations produced by any passerine (*N* = 73 trials). Large dots and error bars show the mean ± SD among trials. "none", "cool", and "warm" refer to no light, cool white light, and warm white light, respectively.

The results were robust in three important ways. First, the average time and average distance to disturbance were not derived from a single species that vocalized earlier than all the rest, but, rather, from the vocalizations of 23 different passerine species (Table 2.2). Second, the effect of noise on distance to disturbance was not driven by the very strong effect seen in Swainson's Thrush (see below), since the results remained identical with respect to statistical significance when Swainson's Thrush was removed from the calculation of distance. Third, the findings were not affected by my choice of inclusion criteria (*i.e.*, that vocalizations were localized to within 30 m of the disturbance with a localization error of 0.02 or less). I re-ran the analyses using all combinations of localization error (0.01, 0.02, 0.03, 0.05, 0.1, no limit) and distance (20, 30, and 40 m) and the results with respect to statistical significance remained similar (Appendix 4). Specifically, birds were always attracted to noise. For five of 18 combinations (distance = 20 x error = 0.02, 0.03, 0.05, no limit; distance = 30 x error = 0.03), there also emerged a statistically significant interaction between noise and light, such that the attractive effect of noise was weakened in the presence of light. For one combination (distance = 40 m x error = no limit), there was also a statistically significant effect of light on distance, such that birds were repelled by the presence of light. Finally, for two combinations (distance = 30 x error = 0.1, no limit), there was a statistically significant effect of light on the average time of the first five vocalizations, such that the presence of light delayed song production.

Single-species Analyses

I conducted species-specific analyses on the six most common species, though I note that sample sizes for these analyses were smaller than for the passerine analysis (Boreal Chickadee, N = 20 arrays; Dark-eyed Junco, N = 36; Ruby-crowned Kinglet, N = 31; Swainson's Thrush, N = 26; White-throated Sparrow, N = 20; Yellow-rumped Warbler, N = 38). I did not apply any adjustments to experimentwise error because the analysis and conclusions for one species are independent of the analysis and conclusions for another species.

The average time of the first five vocalizations was not affected by noise, light, or the interaction between noise and light for five of the six species, including Boreal Chickadee, Dark-eyed Junco, Ruby-crowned Kinglet, Swainson's Thrush, and White-throated Sparrow (2-factor ANOVA: all $F \leq 2.20$, all $p \geq 0.117$; Figure 2.5; complete statistical models in Appendix 3). The only exception was Yellow-rumped Warbler ($F_{3,34}$ = 3.12, p = 0.039), which began vocalizing earlier when noise was present versus absent (coefficients analysis: t = -2.49, p = 0.018; Figure 2.5; Appendix 3). The average distance to disturbance was also not affected by the experimental manipulations for five of the six species, including Boreal Chickadee, Dark-eyed Junco, Ruby-crowned Kinglet, White-throated Sparrow, and Yellow-rumped Warbler (2-factor ANOVA: all $F \leq 2.19$, all $p \geq 0.108$; Figure 2.6; Appendix 3). For Swainson's Thrush, however, there was a statistically significant effect of the disturbance treatments ($F_{3,22}$ = 22.85, $p < 0.001$), with individuals

being attracted to noise (t = -4.38, p < 0.001) and repelled by light (t = 2.97, p = 0.007; Figure 2.6; Appendix 3). There was also a significant interaction between noise and light for Swainson's Thrush (t = -2.99, p = 0.007), with individuals being attracted to the combination of light and noise (Figure 2.6; Appendix 3). Finally, although many of the analyses were not statistically significant, it is worth noting that, for all six species, birds were, on average, closer to the disturbance when noise was present versus absent, which is unlikely to have occurred by chance (Figure 2.6; binomial test: p = 0.031).

Figure 2.5

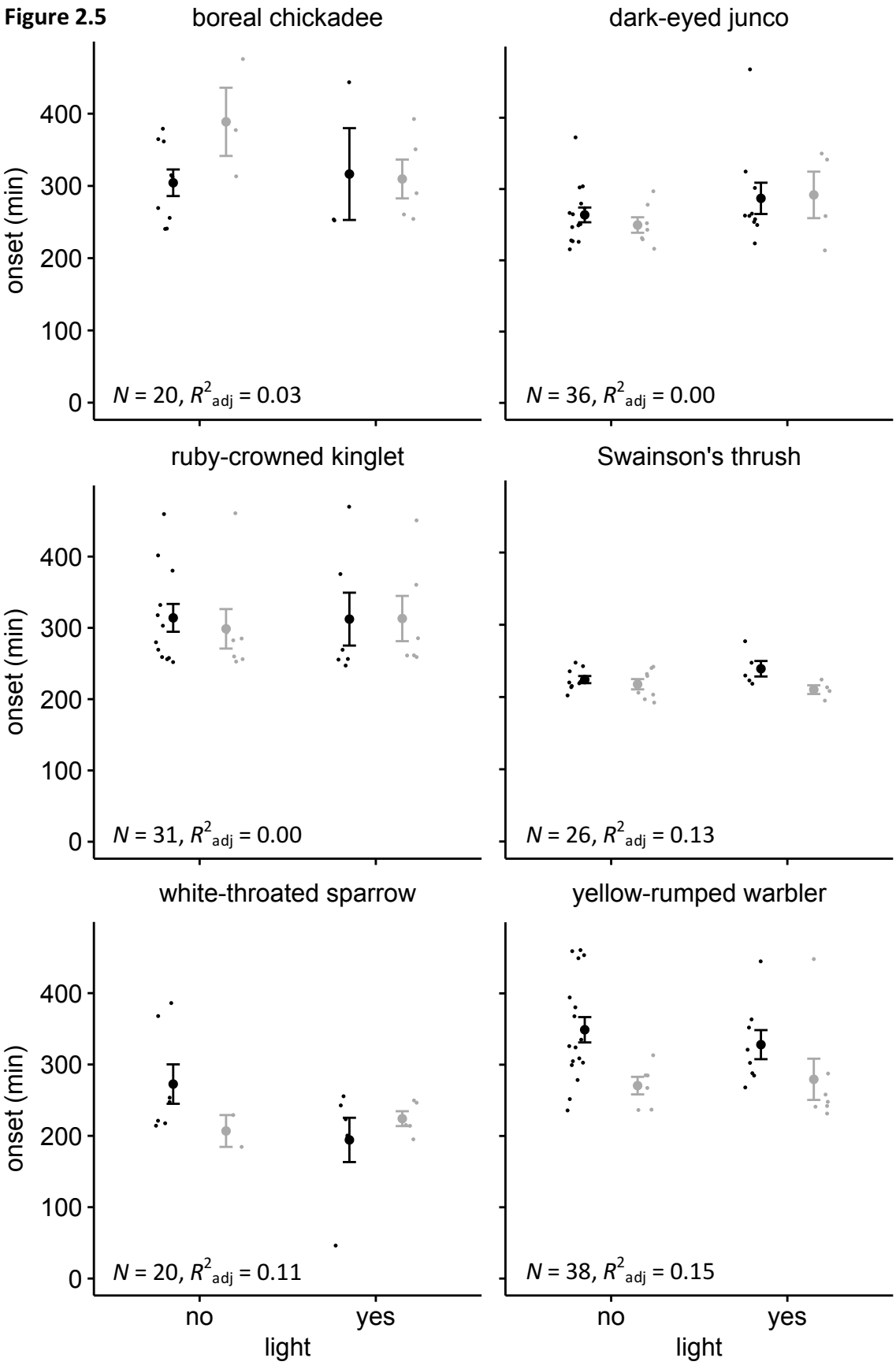
boreal chickadee
dark-eyed junco
ruby-crowned kinglet
Swainson's thrush
white-throated sparrow
yellow-rumped warbler
onset (min)
0
100
200
300
400
N = 20, R2adj = 0.03
N = 36, R2adj = 0.00
N = 31, R2adj = 0.00
N = 26, R2adj = 0.13
N = 20, R2adj = 0.11
N = 38, R2adj = 0.15
no
yes
light

Figure 2.5 The effects of noise (noise absent = black; noise present = grey), light, and the interaction between noise and light on the average time (number of minutes past midnight) of the first five vocalizations produced by each of the six most common species. Large dots and error bars show the mean ± SD. Small dots show the average time of onset for the first five vocalizations of a given trial.

Figure 2.6

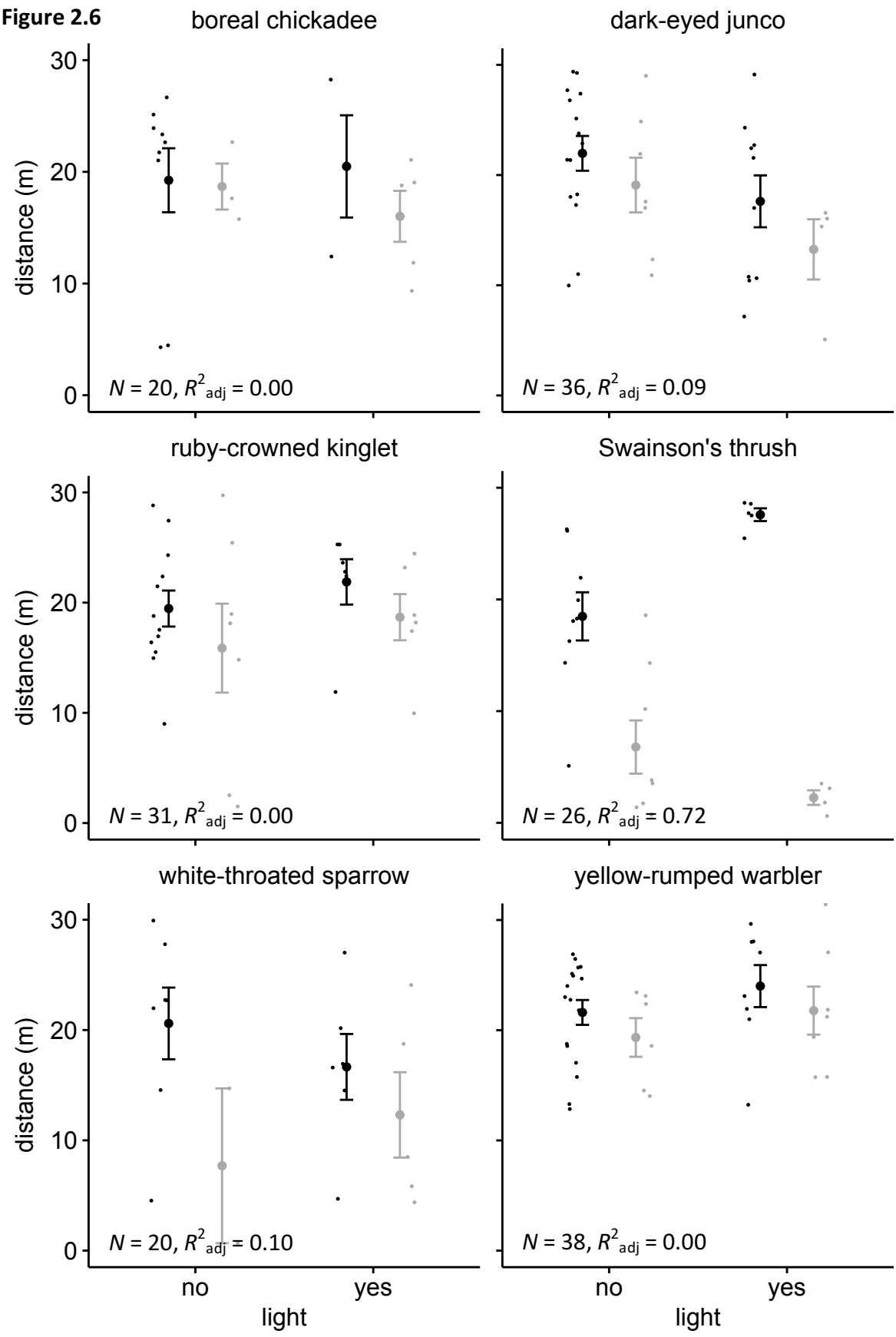
boreal chickadee
dark-eyed junco
ruby-crowned kinglet
Swainson's thrush
white-throated sparrow
yellow-rumped warbler
distance (m)
0
10
20
30
N = 20, R2adj = 0.00
N = 36, R2adj = 0.09
N = 31, R2adj = 0.00
N = 26, R2adj = 0.72
N = 20, R2adj = 0.10
N = 38, R2adj = 0.00
no
yes
light

Figure 2.6 The effects of noise (noise absent = black; noise present = grey), light, and the interaction between noise and light on the average distance to disturbance of the first five vocalizations produced by each of the six most common species. Large dots and error bars show the mean ± SD. Small dots show the average distance to disturbance of the first five vocalizations of a given trial.

Discussion

I experimentally manipulated the presence of anthropogenic noise and light to determine their independent and combined effects on the vocal and spatial behaviour of wild birds. When all passerine species were analyzed together, none of the treatments influenced when birds began vocalizing. However, anthropogenic noise did attract birds to the source of the stimulus. Contrary to my prediction, light did not attract avian species, at least when all colours of light were pooled into a single analysis; depending on the localization settings used, artificial light either repelled birds or had no effect on their spatial behaviour (Appendix 4). When responses to each colour of light were compared, however, there was evidence from five trials that birds were attracted to blue light. The within-species analyses of the six most common boreal bird species revealed similar patterns to the passerine analysis, though most of the effects were not statistically significant. There were two exceptions. Swainson's Thrush was attracted to noise and the combination of noise and light, but was repelled by light when presented in the absence of noise. I also found that Yellow-rumped Warbler began singing earlier in the presence of noise.

Experimental traffic noise attracted passerine birds over spatial scales of 20 to 40 m from the disturbance (Figures 2.3 and 2.6; Appendices 3 and 4). This finding contradicts my prediction that noise would repel birds, which was based on earlier studies. Bayne et al. (2008) found that passerine density in the breeding season was

lower in areas adjacent to noise-generating compressor stations than in control areas adjacent to quiet, but otherwise similar, oil well pads. Similarly, Blickley et al. (2012) found that male Greater Sage-Grouse (*Centrocercus urophasianus*) were less abundant at leks paired with experimentally broadcast traffic noise than at silent control leks. Finally, during both the migratory and breeding seasons, bird densities were lower near both real (Reijnen et al. 1995; Wiacek et al. 2015) and simulated (McClure et al. 2016) roads. A possible explanation for the apparent discrepancies is that all of these other studies measured avian densities next to chronic noise that had begun before birds arrived at the breeding grounds. The density of birds at those sites was likely governed by whether newly arriving migrants (Bayne et al. 2008; Wiacek et al. 2015; McClure et al. 2016) or males establishing leks (Blickley et al. 2012) chose to settle near noisy sites. In contrast, I measured the proximity of resident birds to a noise source that was introduced into their already-established breeding territories. It is therefore possible that birds avoid noisy sites when choosing where to settle, but approach noise when it occurs within or near their already-established breeding territories.

An alternative explanation is that birds approach novel noise stimuli because they are curious, and then avoid those stimuli as the novelty is replaced by chronic exposure. This explanation seems unlikely because my noise stimuli had typically been playing for 11.5 hours before birds began singing, though it is possible that the novelty is only replaced after several days or weeks of exposure. However, the majority of species

included in my analyses were also migratory and had likely encountered traffic noise during previous migrations (Table 2.2; Blumstein 2014). Resident species, including Common Raven, Boreal Chickadee, Red-breasted Nuthatch, Pine Siskin, and Common Redpoll, were detected within my study, so it is possible that the experimental traffic noise was novel to them. However, these species were outnumbered by migratory species, so probably had a relatively small effect on the overall passerine analysis. Future studies comparing the responses of residents and migrants to anthropogenic noise would be valuable.

Noise did not affect when birds began singing, as I had hypothesized. Previous studies examining the effects of traffic noise on the timing of the dawn chorus involved natural traffic noise that fluctuated throughout the day as a function of traffic patterns (*e.g.,* rush hour). The relatively quiet periods that occur between times of heavy traffic may have provided birds in those studies with predictable periods of relief from acoustic masking, which may have prompted them to shift song production to those times (Arroyo-Solis et al. 2013; Cartwright et al. 2014). In my study, the simulated traffic occurred at a constant rate throughout the relatively short playback period (1700 h until 0800 h the following day), thereby providing no predictable cues about when the noise might subside. I also had three different noise stimuli to minimize potential effects of pseudoreplication. All stimuli were of traffic noise, but they included different rates of passing vehicles. It is possible that some species tolerate low levels of noise, and that the

effects of noise on the onset of singing occur only in response to louder noise or higher rates of traffic. For example, some species may adapt to road noise associated with small, rural road traffic, but not to the constant and intense traffic noise associated with major urban freeways (Reijen et al. 1995). Another possible reason for the discrepancy is that these previous studies were correlational in nature, so the reduction in song production during peak traffic times may have been caused by the increased number of vehicles (*e.g.,* because of increased exhaust or increased visual distraction caused by vehicle motion and/or headlights), rather than by the associated increase in noise (Reijen et al. 1995; Kuitunen et al. 1998; Goodwin and Shriver 2011). Additional experimental research is needed to disentangle the effects of noise from the other forms of disturbance that commonly co-occur with noise (*e.g.*, roadways, urban development, vehicles, and exhaust), particularly since the effects of noise on the timing of bird song have been inconsistent in the literature (Fuller et al. 2007; Summers et al. 2011; Arroyo-Solis et al. 2013; Gil et al. 2015; Dominoni et al. 2016; Dorado-Correa et al. 2016; Sierro et al. 2017).

Vocalizing passerines were not attracted to artificial light when the different colours of light were combined into a single treatment for analysis (Figure 2.3). Depending on the localization settings used, birds may even have been repelled by light (Appendix 4). This was surprising because several studies show that birds are attracted to bright lights (but see de Molenaar et al. 2006), such as open fires on beaches

(Maillaird 1898), high-powered beams of light (van Doren et al. 2017), and lights on buildings (McLaren et al. 2018), airplanes (Dolbeer and Barnes 2017), and offshore oil platforms (Montevecchi 2006). However, most of those studies involved birds that were flying during migration or long-distance foraging excursions (Jones and Francis 2003; Ronconi et al. 2015; van Doren et al. 2017; McLaren et al. 2018). In contrast, my study involved passerines in established breeding territories. Most passerines remain within or near their territories throughout the breeding season (Barg et al. 2005), suggesting that attraction to light may occur primarily during long-distance flight. Another possibility is that, compared to the lights used in my study, the lights used in most previous studies were more visible because they were more powerful and were located in open areas (*e.g.*, oil platforms in the open ocean, light projected skyward, urban glow found above cities (Jones and Francis 2003; Dolbeer and Barnes 2017; van Doren et al. 2017). Brighter sources of artificial lighting are noticeable from farther away and can be reflected by low cloud cover or fog to create an even larger area of illumination (Gauthreaux and Belser 2006; Merkel and Johansen 2011; van Doren et al. 2017). In contrast, the lights used in my study were less powerful and were located below the canopy of a dense boreal forest. Furthermore, the birds in my study were likely singing from perches located below the top of the canopy (Krams 2001; Barg et al. 2005), where visibility would have been reduced. I did find some evidence that birds are attracted to blue light, but that evidence was based on only five trials, so should be interpreted with caution, especially

since most previous studies have shown that birds are not attracted to blue light as strongly as other colours, such as red (Poot et al. 2008, Dolbeer and Barnes 2017).

Artificial lighting did not cause passerine birds to begin singing earlier, which contrasts with several previous studies (Gauthreaux and Belser 2006; Fuller et al. 2007; Kempenaers et al. 2010; Dominoni et al. 2013; Watson et al. 2016; van Doren et al. 2017). However, those studies compared birds living in brightly lit cities to birds living in rural areas with few or no lights. In contrast, my study compared birds' responses to a single dim light versus no light, so the magnitude of the light treatment was much weaker in my study than in those previous studies. Interestingly, Da Silva et al. (2017) used low-intensity lighting, similar to that used in my study, and also failed to detect an effect on the onset of dawn song. Together, these studies suggest that the brightness, not just the presence, of artificial lighting may be important in stimulating birds to sing prematurely. This is consistent with Thomas et al. (2002), which showed that species with larger eyes that are more sensitive to dim light begin signing earlier in the morning, as compared to avian species with smaller eyes. For example, thrushes, such as Swainson's Thrush, have larger eyes compared to other songbird species of similar size and may also begin singing earlier in the day (Thomas et al. 2002).

My species-specific analyses revealed both similarities and differences to my overall passerine analysis. First, the species-level analyses supported the finding that

passerines are generally attracted to traffic noise. Although the analyses of individual species were generally non-significant (Appendix 3), birds from all six species were closer, on average, to the noise stimulus than to the silent control (Figure 2.6), which is unlikely to have occurred by chance. Second, Swainson's Thrush was attracted to noise and repelled by light. Passerines were also attracted to noise and, depending on the localization settings, repelled by light, but the effects were much stronger in Swainson's Thrush. Of the six species analyzed, Swainson's Thrush is the only one classified as an interior forest specialist (Whitaker and Montevecchi 1999). The other five species are categorized as 'forest generalists' (Boreal Chickadee and Ruby-crowned Kinglet), 'open-edge species' (Dark-eyed Junco, White-throated Sparrow), or 'ubiquitous species' (Yellow-rumped Warbler), which all include or tolerate anthropogenic edge habitat in their breeding range. Therefore, habitat specialization and avoidance of disturbed habitat may make Swainson's Thrush more sensitive and responsive to habitat disturbances that occur suddenly within their breeding territories (St. Clair 2003; Blumstein 2006; Bonier et al. 2007). Another possibility is that, because Swainson's Thrush forages on the ground (Holmes and Robinson 1988), it may have been more exposed than the canopy-dwelling species to the light and noise stimuli. Third, unlike passerines in general, Yellow-rumped Warblers sang earlier when noise was present. Yellow-rumped Warblers are one of the first warbler species to begin singing in the morning (Morse 1989), so it is possible that the forest was quieter, and the traffic noise

more obvious, when they began singing, as compared to when most species began singing.

My living laboratory approach provided experimental control and passive monitoring of 31 species of free-living birds in a natural context, but it also had several limitations. First, microphone arrays can only detect and localize vocalizing animals, so it is possible that my study missed non-vocal responses to experimental treatments. This could not account for the observed attraction to noise, relative to the silent control or light-only treatment, but could potentially explain my negative results, such as the unexpected finding that birds were generally not attracted to light. For example, some birds might have approached the light stimulus in silence, while others remained distant and singing. Direct observation could reveal non-vocal responses, but would be challenging because of the low light levels that exist in the forest when the dawn chorus begins. Radio telemetry might overcome the challenge of observing birds in dim light, but such studies are labour-intensive and often lead to small sample sizes. Radio telemetry also requires birds to be captured and fitted with transmitters, which can affect their behaviour (Mech and Barber 2002; Lee and Marsden 2008). A second limitation of my study is that my playback equipment needed to be portable, which limited the intensity of my noise and light stimuli. However, all noise and light attenuate with increasing distance from their source, thereby forming intensity gradients. Although my stimuli did not replicate the maximum intensities of light and noise that

might be found sporadically in the environment, they undoubtedly simulated intensities that many free-living animals experience (*e.g.,* those living close to low-intensity disturbances and those living far away from high-intensity disturbances).

Conservation of avian populations includes mitigating the effects of anthropogenic disturbances, such as noise and artificial lighting. Often, multiple forms of disturbance occur simultaneously, so it can be difficult for managers to know which disturbances actually affect animals and which ones should be mitigated. I found that passerine birds are attracted to traffic noise, but not to light, which often accompanies traffic noise (*e.g.*, streetlights, vehicle headlights). If birds are drawn to traffic noise, then they may experience an increased likelihood of fatal collision with vehicles at roadsides (Kociolek et al. 2011; Loss et al. 2014). Although anecdotal, I observed many dead passerines that had been struck by vehicles along the roadways connecting my study sites (personal observation). Another concern is that attraction to traffic noise may cause birds to reside near roadsides, which may negatively affect their reproductive success (Leonard and Horn 2008; Nemeth and Brumm 2010; Halfwerk et al. 2011b; Hanna et al. 2011; Blickley et al. 2012; Meillere et al. 2015; Potvin et al. 2016; Derryberry et al. 2017) or increase their predation risk (Delaney et al. 1999; Quinn et al. 2006; Meillere et al. 2015) through the masking of acoustic signals. Being attracted to traffic noise could also increase exposure to air pollution from vehicle exhaust or the risk of poisoning through the consumption of de-icing agents (Kociolek et al. 2011). My study

suggests that conservation biologists and land managers should consider the effects of noise on birds, as well as the use of noise mitigation technologies that reduce noise in vulnerable or ecologically important habitat.

In conclusion, my study is the first to my knowledge to use microphone arrays to test the independent and combined effects of anthropogenic light and noise on the singing and spatial behaviour of wild birds. This promising technology allowed me to passively and accurately quantify the responses of 31 species over a prolonged period of time (8 hours per trial) and across a broad geographic area (110 sites with blanket coverage over a 30-m radius at each site, or approximately 31 ha). My results show that birds in the boreal forest are attracted to traffic noise, but not to most artificial lighting, and that attraction to noise is taxonomically widespread.

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Chapter 3: Implications for our Understanding of Avian Responses to Anthropogenic Noise and Light

Summary of Findings

During the 2016 and 2017 avian breeding seasons (May-June), I tested whether anthropogenic noise and artificial lighting affected the singing and spatial behaviour of passerine birds in the region surrounding Happy Valley-Goose Bay, Labrador, Canada. I hypothesized that noise would repel birds and that light would attract them. I also hypothesized that light would advance the onset of the dawn chorus. I sampled 110 sites in undisturbed boreal forest using an 8-channel microphone array that provided blanket coverage of an approximately 40 x 40 m area (0.16 ha). In the middle of each array, I broadcasted one of four experimental treatments (noise, light, noise and light, no noise or light) throughout a single night and recorded all avian vocalizations produced inside the array over this time. I assigned each vocalization to species, noted when it was produced, and used acoustic localization to determine where it had been produced in relation to the experimental stimulus.

My results show that passerines were attracted to noise stimuli, but were neither attracted nor repelled by light stimuli when all colours were combined. However, evidence from five trials suggests that birds may have been attracted to blue light, but further testing is required to confirm that result. None of the treatments affected the

onset of dawn song. Species-specific analyses of the six most common species revealed similar patterns to the passerine analysis, though a few differences did emerge. Specifically, Yellow-rumped Warbler began vocalizing earlier when noise was present, and Swainson's Thrush was repelled by light.

My findings are inconsistent with previous studies on the effects of anthropogenic noise and light on birds. For example, several previous studies showed that birds avoid anthropogenic noise (Delaney et al. 1999; Blickley et al. 2012; McLaughlin and Kunc 2013; McClure et al. 2016), whereas my results show that passerine birds in general are attracted to noise. One possible explanation for this discrepancy is that attraction to noise may vary throughout the year. For example, birds might be repelled by noise when choosing where to establish their breeding territories, but attracted to noise when it occurs suddenly from within their already-established territories. Indeed, most previous studies focused on the migration season, when birds were moving across large areas while choosing where to establish their territories (Gauthreaux and Belser 2006; Wiacek et al. 2015; McClure et al. 2016; van Doren et al. 2017).

Like noise, lights also affect birds, with most studies showing that birds are attracted to light (Smit and Visser 1993; Jones and Francis 2003; Montevecchi 2006; Poot et al. 2008; Rodriguez et al. 2015, 2017; Ronconi et al. 2015; Watson et al. 2016;

Dolbeer and Barnes 2017; van Doren et al. 2017; McLaren et al. 2018). In contrast, I found that light did not attract birds, and that, for Swainson's Thrush, it actually repelled them. My findings are consistent with only one previous study, which showed that lighting had no effect on 14 species of European songbirds (Silva et al. 2017). A possible explanation for why light did not affect birds in my study, or in Silva et al. (2017), is that both of these studies used relatively dim lights, such as those found on homes and cottages. Combined with the dense forest at my sites, it is possible that my lights were not visible over a large enough distance to produce detectable attraction by birds. In comparison, most previous studies used intense lights in open areas, where the lights were visible over long distances. My findings remain relevant, however, since the majority of lights on the landscape are dim lights associated with homes, businesses, cottages, and residential street lighting (NOAO 2018). My finding that birds appear to be attracted to blue light is inconsistent with previous studies, which indicate a stronger fixation to red light (Poot et al. 2008; Dolbeer and Barnes 2017). However, given the small number of samples involving blue light, my results should be interpreted with caution and further evaluated in future studies involving multi-coloured light types and avian behaviour.

Implications for Labrador Avifauna

The boreal forest habitat is of ecological importance to breeding birds, with significant numbers of individuals and species migrating there each summer to breed

(Rosenberg et al. 2016). For example, of the 37 warbler species found in Canada, 50% occupy the boreal forest during the avian breeding season (Downes et al. 2011). The forests of Newfoundland and Labrador compose 7% of the 5,520,000 km^2 of boreal forest within Canada (Boreal Songbird Initiative 2018), with the majority being from within Labrador. Indeed, more than 60% of Labrador – an area of 288,000 km^2 – is comprised of intact boreal forest (Roberts et al. 2006). Approximately 152 landbirds are known to occur regularly in Labrador (Roberts et al. 2006), and 259 landbirds have been detected at least once within the region (Cornell Lab of Ornithology 2018).

Labrador is also a primary economic region for Canada due to its significant investment in hydroelectric development, mining, forestry, and agriculture (Urquizo et al. 2000). These activities remove avian habitat and create other forms of disturbance, such as noise and light, which affect avian behaviour (*e.g.*, Ortega 2012). Furthermore, these developments occur on a large scale in Labrador. Hydroelectricity from Labrador, for example, supplies most of the province's energy demands (Nalcor Energy 2018a). The Churchill Falls hydroelectric generating plant, which is one of only four in Labrador, is one the largest in the world, with its associated reservoirs covering a total landmass of 5700 km^2 (Nalcor Energy 2018a). The mining industry currently employs 6,111 individuals within Labrador, or approximately 20% of Labrador's population (Roberts et al. 2006; Department of Natural Resources 2018a), and was valued at $3,393,871 in regard to gross shipments in 2018 (Department of Natural Resources 2018b). There are currently 11 active mining projects in Labrador, the largest of which is the Carol Project

operated by the Iron Ore Company of Canada, which is approximately 11,000 ha in size, including mining pits, tailings, waste, concentrator and pellet plants, infrastructure, transport, and conveyors (Government of Newfoundland and Labrador 2018a). In addition to land conversion, these industries create multiple forms of disturbance, including artificial light and noise, that, together, cause significant declines in avian populations (Downes et al. 2011; Rosenberg et al. 2016).

Despite a large scientific literature on the effects of anthropogenic disturbance on birds, and despite Labrador's expansive avian breeding grounds and growing industrial development, very few studies on how anthropogenic disturbance affects birds have been conducted in Labrador (for exceptions, see Simon et al. 2000; Schwab et al. 2006; Whitaker 2017). However, there have been several surveys of avian diversity, particularly in the region surrounding the towns of Happy Valley-Goose Bay, where I conducted my study (Sullivan et al. 2009; Nalcor 2018b).

My study contributes to the existing knowledge base concerning avian species richness and distribution in Labrador, as I detected 31 songbird species during the construction of the Muskrat Falls hydroelectric project. In comparison, an environmental assessment conducted by Nalcor Energy between 2006–2016 (*i.e.,* prior to and during the construction of the Muskrat Falls project in Labrador) reported 46 passerine species within the lower Churchill Falls region (Nalcor Energy 2018c). The difference in species

richness may be due to differences in the habitat types sampled, as the Nalcor Energy report included habitat types that I did not sample due to logistical constraints (wetlands and riparian zones).

Finally, my study includes an archive of natural sounds from Labrador that will be made available through the digital repository of Memorial University of Newfoundland's Queen Elizabeth II Library. To my knowledge, this is the first digital collection of natural sounds, including local avifauna species, from Labrador. It will allow future researchers to assess species richness and the distributions of individual species across my study area during the 2016 and 2017 avian breeding seasons, and may thus provide an important benchmark and historical information that will allow researchers to determine how species richness changes in this region over time. The archive will include vocalizations from passerines, but also from non-passerine birds, mammals, amphibians, and invertebrates.

Future Directions

My experiment used acoustic localization to test whether anthropogenic noise and light influence avian singing and spatial behaviour. Advantages of this approach are that it operates autonomously for relatively long periods, reduces observer interference, and provides spatial information and a permanent audio record that can be reviewed and archived. A limitation is that birds are not detected if they remain silent.

Fortunately, most passerine species vocalize regularly throughout the breeding season, so it is unlikely that they would have remained undetected throughout my long recordings I analyzed from midnight to 8 the following morning. However, it is possible that non-vocal responses occurred and remained undetected. For example, birds might have approached lights in silence and resumed singing only after they had returned to their original locations. Therefore, the results of acoustic localization studies should be combined with those generated by other methodologies to fully characterize behavioural responses to disturbance. For example, individual birds equipped with spatial tracking devices could provide insight into silent spatial responses, though such studies would be labour-intensive and would likely be limited to small sample sizes from only a few species.

Although my study included multiple noise and light stimuli, I lacked the statistical power needed to make meaningful comparisons among different types of traffic noise or among different colours or intensities of light. Notably, the strong effect of noise on avian spatial behaviour suggests that additional studies are needed to determine which aspects of noise attract birds. For example, future studies could manipulate noise amplitude, the frequency of passing vehicles, and noise type (*e.g.*, small or large vehicles, automobiles versus air traffic, industrial versus traffic noise). Similarly, future studies should use a standard approach to examine the effects of noise on avian spatial behaviour at different times of the year, since my results suggest that

migrating and territorial birds respond differently to noise. With respect to light, future studies should investigate the attractive effects of blue light, since evidence from five of my trials suggests that birds may be attracted more strongly to blue light than to the other colours tested in my study.

While my study shows that noise attracts birds, it is also possible that noise affects birds in ways I did not measure. For instance, noise may impair an individual's ability to detect oncoming vehicles and may, therefore, increase their risk of collision after attracting them to roadsides. Although anecdotal, I found many dead birds along roadsides while traveling to my study sites. Noise can also mask cues associated with predators (*e.g.,* alarm signals; Templeton et al. 2016), so being attracted to point sources of noise could further reduce survival through increased predation risk. Finally, previous research has shown that birds experience reduced reproductive success in noisy environments (*e.g.*, Potvin et al. 2016); being attracted to noisy locations may exacerbate this effect.

In conclusion, my study is the first to my knowledge to use a living laboratory approach to study the independent and combined effects of anthropogenic noise and light on birds. My results show that traffic noise during the breeding season attracts birds and may thus pose a risk to them during this critical time of year.

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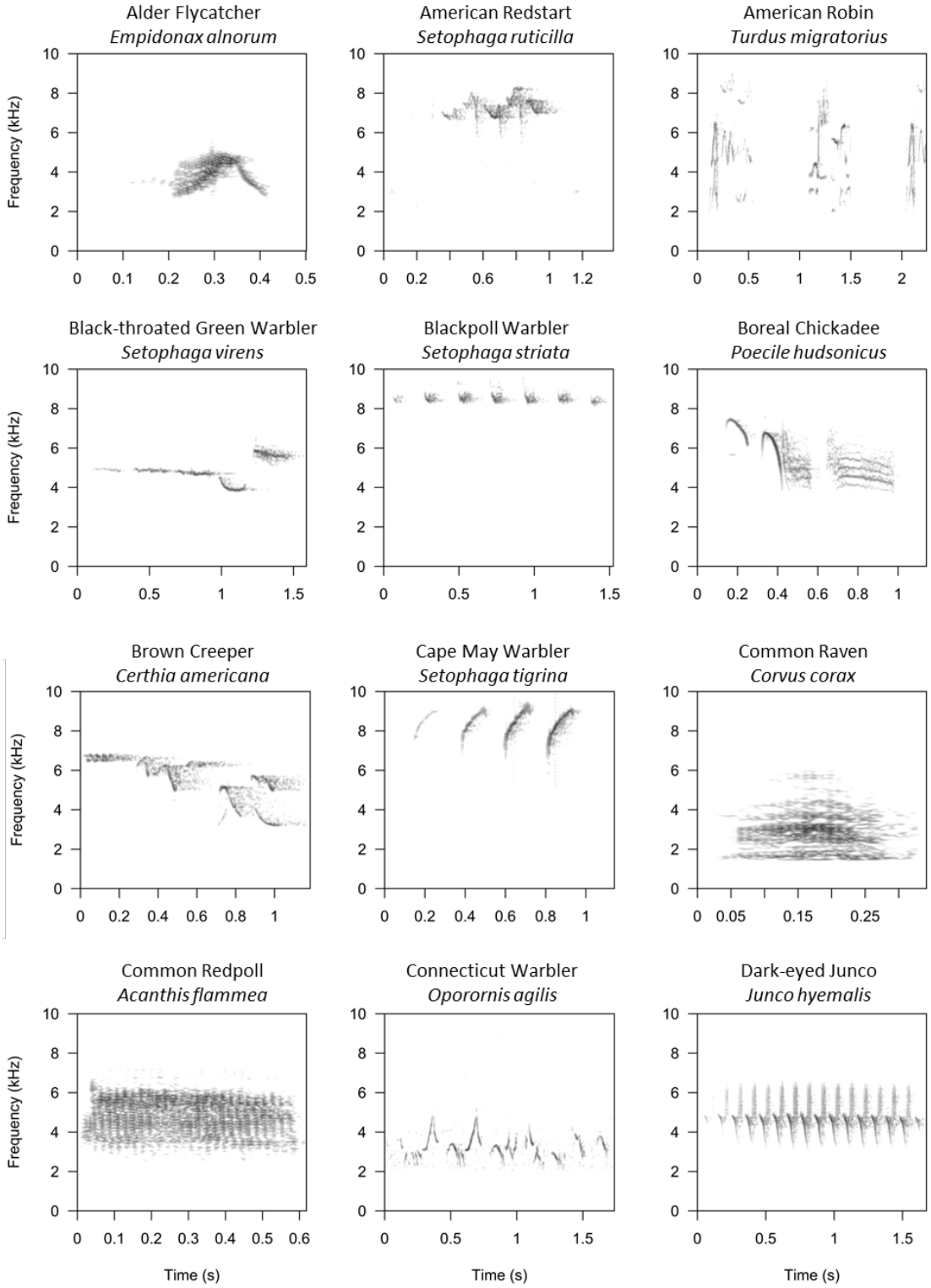
Appendices

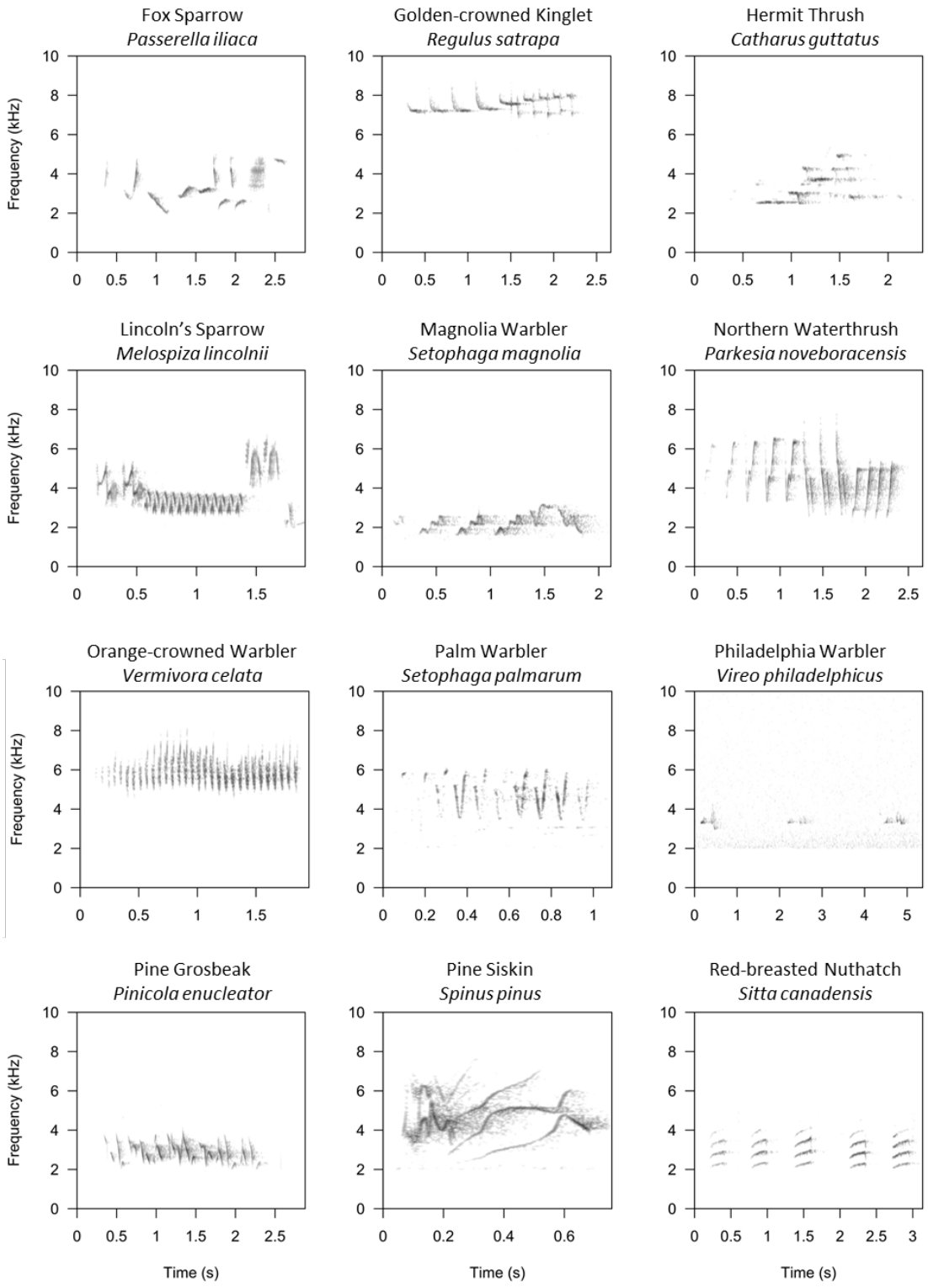
Appendix 1. Summary of experimental disturbance treatments (no noise and no light, noise but no light, light but no noise, or noise and light), including the specific stimuli used (noise variant and/or light colour) and sample sizes, for data collected during the 2016 and 2017 avian breeding seasons in Labrador, Canada.

Treatment	Stimulus		# trials
Control	none		39
Noise (17 trials)	low		7
	medium		7
	high		3
Light (35 trials)	cool white		8
	warm white		6
	blue		5
	red		9
	green		7
Noise + Light (19 trials)	low	cool white	2
		warm white	0
		blue	1
		red	1
		green	2
	medium	cool white	1
		warm white	2
		blue	1
		red	3
		green	1
	high	cool white	2
		warm white	1
		blue	2
		red	0
		green	1

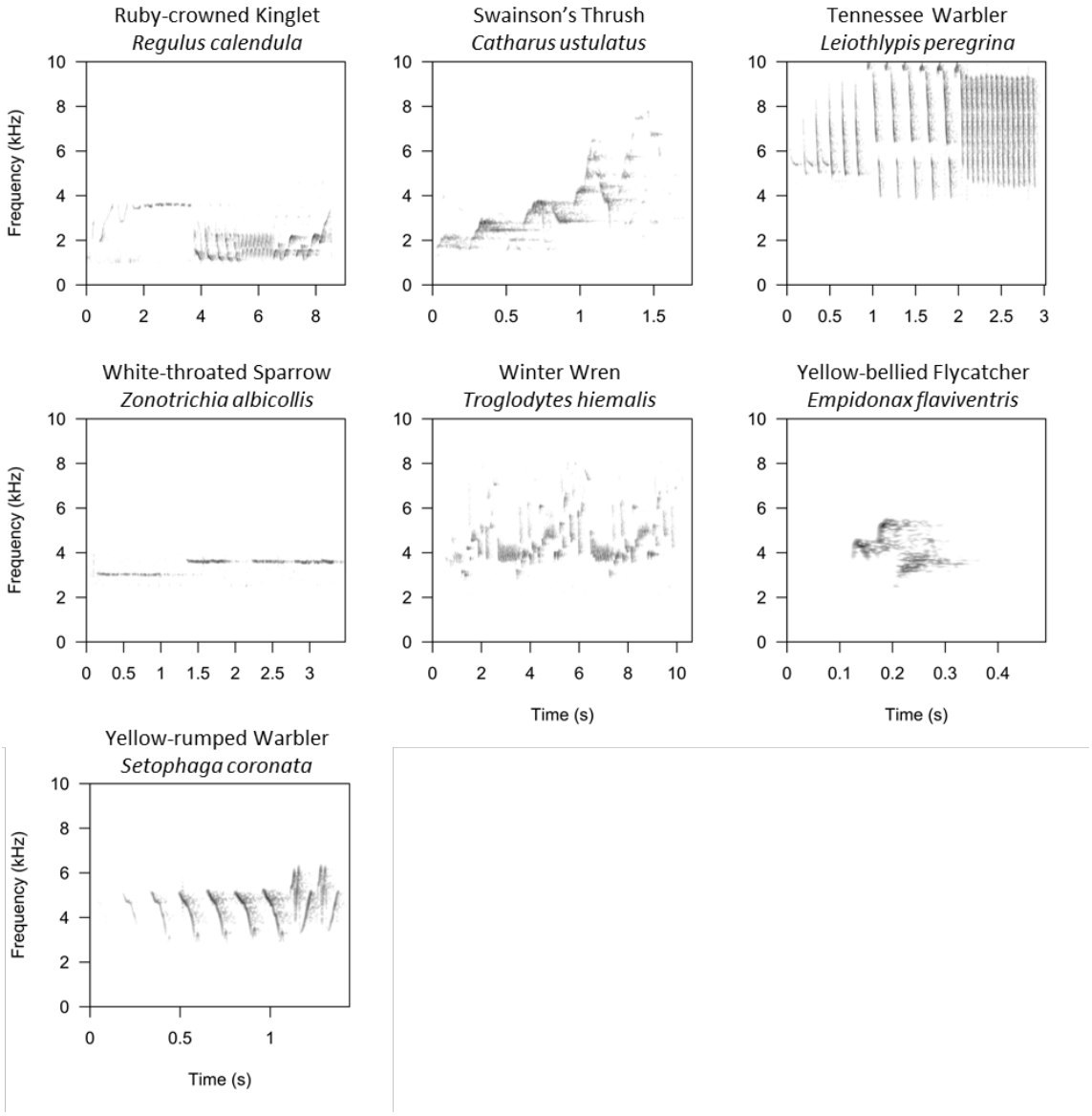
Appendix 2. Spectrograms of the species-specific vocalizations (31 species) for the time of first vocalization and distance from stimuli analyses.



Appendix 2 (continued)



Appendix 2 (continued)



Appendix 3. Summary of statistical analyses. 2-factor ANOVAs were used to test the effects of noise, light, and the interaction between noise and light on the average time of onset and the average distance to disturbance of the first five vocalizations produced. In one set of analyses (labeled below as 'All Passerines'), the dependent variables were based on all Passerines. In a second set of analyses, the dependent variables were calculated and analyzed separately for each of the six most common species, as determined by the proportion of arrays in which at least one individual was localized to within 30 m of the disturbance (or of the centre of the array in control trials) with a localization error of 0.02 or less. Significance of the overall model was tested using an *F* statistic, whereas significance of model coefficients was tested using *t* statistics. Where the overall model is significant, statistically significant coefficients are in bold.

	time of onset		distance to disturbance	
model	statistic	p-value	statistic	p-value
All Passerines (*N* = 89)				
overall model	0.29	0.832	**14.05**	**< 0.001**
intercept	20.44	< 0.001	**19.53**	**< 0.001**
noise	0.48	0.636	**-5.64**	**< 0.001**
light	0.79	0.430	0.09	0.929
noise x light	-0.85	0.397	1.77	0.081

Boreal Chickadee (*N* = 20)				
overall model	1.18	0.348	0.30	0.825
intercept	13.21	< 0.001	7.94	< 0.001
noise	1.83	0.089	-0.12	0.909
light	0.26	0.797	0.26	0.801
noise x light	-1.33	0.201	-0.54	0.595
Dark-eyed Junco (*N* = 36)				
overall model	1.06	0.381	2.19	0.108
intercept	19.99	< 0.001	13.00	< 0.001
noise	-0.61	0.548	-0.96	0.344
light	1.11	0.274	-1.63	0.113
noise x light	0.50	0.622	-0.30	0.764
Ruby-crowned Kinglet (*N* = 31)				
overall model	0.07	0.976	0.84	0.482
intercept	14.40	< 0.001	9.74	< 0.001
noise	-0.43	0.672	-1.09	0.285
light	-0.05	0.963	0.70	0.491
noise x light	0.29	0.777	0.08	0.940

Swainson's Thrush (*N* = 26)				
overall model	2.20	0.117	**22.85**	**< 0.001**
intercept	36.83	< 0.001	**10.09**	**< 0.001**
noise	-0.73	0.476	**-4.38**	**< 0.001**
light	1.47	0.155	**2.97**	**0.007**
noise x light	-1.49	0.151	**-2.99**	**0.007**
White-throated Sparrow (*N* = 20)				
overall model	1.80	0.189	1.72	0.204
intercept	11.39	< 0.001	6.55	< 0.001
noise	-1.30	0.214	-1.93	0.071
light	-2.22	0.041	-0.85	0.407
noise x light	1.50	0.153	1.02	0.322
Yellow-rumped Warbler (*N* = 38)				
overall model	**3.12**	**0.039**	1.02	0.396
intercept	**21.76**	**< 0.001**	17.91	< 0.001
noise	**-2.49**	**0.018**	-0.96	0.343
light	-0.74	0.467	1.12	0.270
noise x light	0.64	0.527	0.01	0.989

Appendix 4. Effects of sampling area radius and localization error on statistical analyses. Sampling area radius is the distance from disturbance (or from the centre of the array in control trials) over which vocalizations were considered for inclusion in the analysis. Localization error is a unitless measure of model fit derived from the localization procedure. For each combination of sampling area radius (20, 30, 40 m) and localization error (0.01, 0.02, 0.03, 0.05, 0.1, no limit), a 2-factor ANOVA tested for effects of noise, light, and the interaction between noise and light on the average time of onset and the average distance to disturbance of the first five vocalizations produced by birds of the order Passeriformes. Where the overall model is significant ($\propto = 0.05$), statistically significant effects are in bold. Degrees of freedom are in parentheses.

	time of onset		distance to disturbance	
model	statistic	p-value	statistic	p-value
Sampling area radius = 20 m; localization error ≤ 0.01				
overall model (3, 60)	0.49	0.690	**4.24**	**0.009**
intercept	14.73	<0.001	**13.37**	**< 0.001**
noise	-0.18	0.856	**-3.43**	**0.001**
light	1.00	0.322	-0.67	0.506
noise x light	-0.44	0.658	1.65	0.104

Sampling area radius = 20 m; localization error ≤ 0.02				
overall model (3, 70)	0.74	0.533	**7.74**	**< 0.001**
intercept	16.78	< 0.001	**15.82**	**< 0.001**
noise	-0.10	0.918	**-4.63**	**< 0.001**
light	0.92	0.359	-1.50	0.137
noise x light	-0.99	0.326	**2.20**	**0.031**
Sampling area radius = 20 m; localization error ≤ 0.03				
overall model (3, 74)	0.88	0.451	**9.61**	**< 0.001**
intercept	16.54	< 0.001	**16.69**	**< 0.001**
noise	0.04	0.968	**-5.00**	**< 0.001**
light	1.27	0.209	-1.39	0.168
noise x light	-1.09	0.280	**2.07**	**0.042**
Sampling area radius = 20 m; localization error ≤ 0.05				
overall model (3, 80)	2.53	0.063	**10.58**	**< 0.001**
intercept	18.53	< 0.001	**17.81**	**< 0.001**
noise	0.44	0.660	**-5.23**	**< 0.001**
light	2.31	0.023	-1.27	0.208
noise x light	-2.05	0.044	**2.06**	**0.043**
Sampling area radius = 20 m; localization error ≤ 0.1				
overall model (3, 89)	0.78	0.508	**11.60**	**< 0.001**
intercept	20.40	< 0.001	**19.35**	**< 0.001**

noise	-0.23	0.820	**-4.93**	**< 0.001**
light	0.76	0.449	-0.80	0.427
noise x light	-0.92	0.361	1.13	0.264
Sampling area radius = 20 m; localization error = no limit				
overall model (3, 98)	2.16	0.098	**6.98**	**< 0.001**
intercept	21.75	< 0.001	**21.32**	**< 0.001**
noise	-0.86	0.391	**-4.41**	**< 0.001**
light	1.32	0.189	-0.92	0.360
noise x light	-0.94	0.348	**2.36**	**0.020**
Sampling area radius = 30 m; localization error ≤ 0.01				
overall model (3, 76)	0.56	0.645	**11.54**	**< 0.001**
intercept	20.27	< 0.001	**17.72**	**< 0.001**
noise	-0.52	0.605	**-5.22**	**< 0.001**
light	0.60	0.550	0.36	0.717
noise x light	-0.49	0.624	1.87	0.065
Sampling area radius = 30 m; localization error ≤ 0.03				
overall model (3, 90)	0.86	0.465	**15.42**	**< 0.001**
intercept	21.34	< 0.001	**21.09**	**< 0.001**
noise	0.32	0.752	**-5.94**	**< 0.001**
light	1.41	0.161	-0.05	0.963
noise x light	-1.15	0.253	**2.03**	**0.046**

Sampling area radius = 30 m; localization error ≤ 0.05				
overall model (3, 96)	1.36	0.261	**12.82**	**< 0.001**
intercept	23.14	< 0.001	**21.05**	**< 0.001**
noise	-0.31	0.757	**-4.92**	**< 0.001**
light	1.45	0.150	0.47	0.637
noise x light	-0.99	0.326	0.92	0.360
Sampling area radius = 30 m; localization error ≤ 0.1				
overall model (3, 99)	**2.92**	**0.038**	**10.86**	**< 0.001**
intercept	**23.70**	**< 0.001**	**22.73**	**< 0.001**
noise	-0.50	0.616	**-4.58**	**< 0.001**
light	**2.47**	**0.015**	-0.04	0.965
noise x light	-0.87	0.386	0.84	0.404
Sampling area radius = 30 m; localization error = no limit				
overall model (3, 103)	**3.02**	**0.033**	**8.96**	**< 0.001**
intercept	**33.63**	**< 0.001**	**27.10**	**< 0.001**
noise	-0.80	0.424	**-4.28**	**< 0.001**
light	**2.18**	**0.031**	-0.36	0.722
noise x light	-0.94	0.350	0.99	0.326

Sampling area radius = 40 m; localization error ≤ 0.01				
overall model (3, 85)	1.18	0.322	**11.54**	**< 0.001**
intercept	24.01	< 0.001	**17.72**	**< 0.001**
noise	-0.32	0.750	**-5.22**	**< 0.001**
light	1.07	0.289	0.36	0.717
noise x light	-1.08	0.282	1.87	0.065
Sampling area radius = 40 m; localization error ≤ 0.02				
overall model (3, 96)	0.53	0.664	**12.11**	**< 0.001**
intercept	23.36	< 0.001	**16.77**	**< 0.001**
noise	0.96	0.337	**-4.79**	**< 0.001**
light	1.05	0.298	1.31	0.195
noise x light	-1.16	0.251	1.56	0.123
Sampling area radius = 40 m; localization error ≤ 0.03				
overall model (3, 97)	0.40	0.752	**13.49**	**< 0.001**
intercept	22.73	< 0.001	**18.84**	**< 0.001**
noise	0.15	0.880	**-4.99**	**< 0.001**
light	1.05	0.297	1.14	0.258
noise x light	-0.56	0.578	1.19	0.237

Sampling area radius = 40 m; localization error ≤ 0.05				
overall model (3, 100)	1.10	0.354	**8.64**	**< 0.001**
intercept	25.49	< 0.001	**18.89**	**< 0.001**
noise	-1.22	0.226	**-3.54**	**0.001**
light	0.70	0.483	1.22	0.225
noise x light	0.69	0.492	0.14	0.892
Sampling area radius = 40 m; localization error ≤ 0.1				
overall model (3, 101)	1.17	0.325	**7.03**	**< 0.001**
intercept	27.54	< 0.001	**19.09**	**< 0.001**
noise	-1.06	0.293	**-2.98**	**0.004**
light	0.97	0.334	1.24	0.216
noise x light	0.47	0.640	-0.17	0.865
Sampling area radius = 40 m; localization error = no limit				
overall model (3, 103)	0.458	0.712	**8.01**	**< 0.001**
intercept	36.50	< 0.001	**24.30**	**< 0.001**
noise	-0.58	0.565	**-2.76**	**0.007**
light	0.70	0.483	**2.03**	**0.045**
noise x light	0.00	0.999	-0.53	0.599